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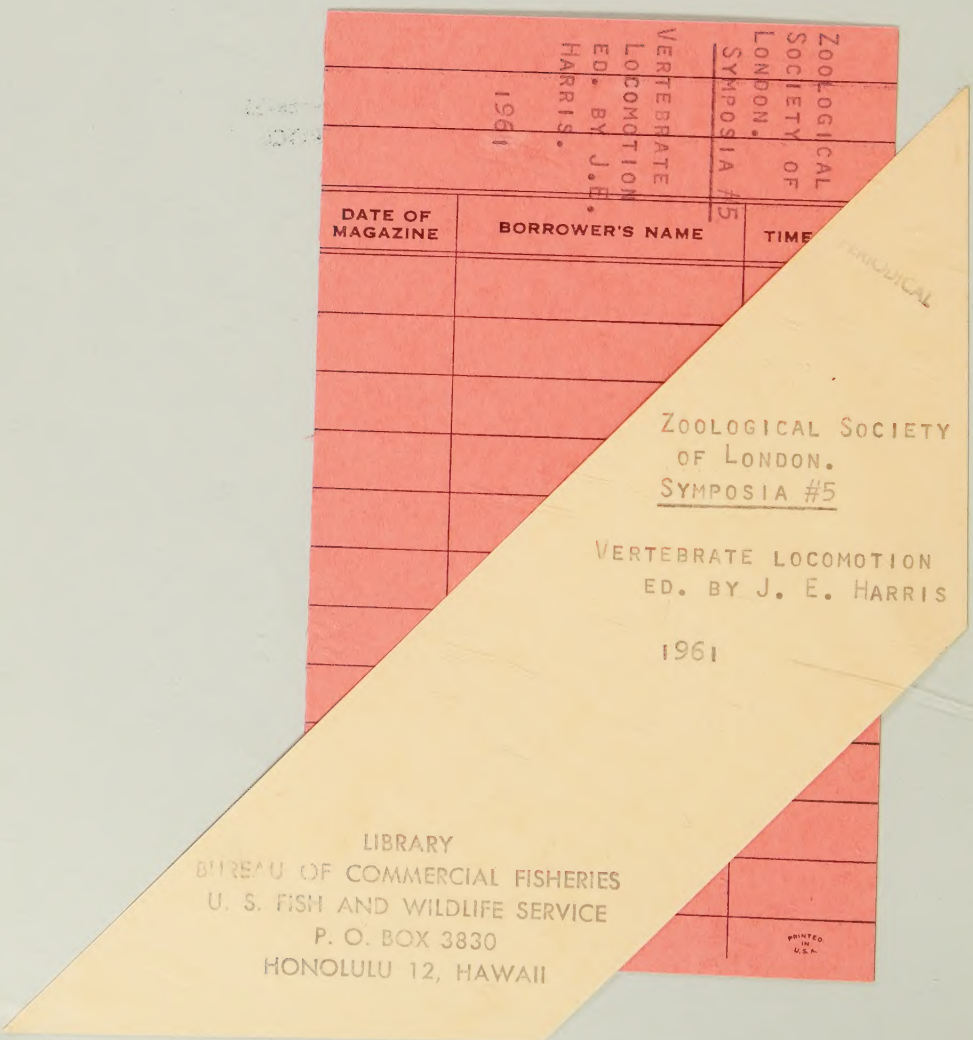
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VERTEBRATE LOCOMOTION

Proceedings of a Symposium held at
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on 9th November, 1960

Edited on behalf of
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J. E. HARRIS

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CONTENTS

Page

Introduction
By J. E. Harris ix

General principles of vertebrate locomotion 1
By James Gray

Problems of fish locomotion 13
By Richard Bainbridge

A note on the shape of fish myotomes 33
By G. M. Jarman

The relationship of fish locomotion to the design of ships 37
By E. H. Watts

Pelvic girdle in amphibian locomotion 43
By H. P. Whiting

Locomotion of seals with particular reference to the forelimb 59
By K. M. Backhouse

Locomotion and locomotory organs in whales and dolphins (Cetacea) 77
By E. J. Slijper

The power requirements of birds in flight 95
By R. H. J. Brown

Aspects of equine and canine locomotion 101
By C. W. Ottaway

Prehensility and opposability in the hands of primates 115
By J. R. Napier

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INTRODUCTION

BY

J. E. HARRIS

University of Bristol

The subject of animal locomotion has attracted a great deal of interest in recent years and it is peculiarly appropriate that Sir James Gray, who has done so much to advance our knowledge in this field, should himself contribute the opening synoptic paper. The Zoological Society provides an excellent milieu for such a topic, combining as it does the scientific interest, whether morphological or physiological, with the purely observational side, the value of which is clearly brought out in several of the contributions to the discussion.

So diffuse a subject cannot hope to be treated exhaustively or even systematically. There are few sweeping generalisations to be made about the mechanisms involved, even within the restricted pattern of organisation provided by the vertebrates. What may interest us, though it should not surprise us, is the implication in several of the subsequent papers of the very high mechanical efficiency of the locomotory process, certainly in swimming and flight, and perhaps also in terrestrial locomotion as well. Three-hundred million years of trial and error is a not inconsiderable time in which to develop an efficient piece of machinery, and if there is still much which our engineers could learn from vertebrate locomotion, it seems probable that, as in so many other cases, the zoologist will only discover how it is done, after the engineer or physicist has independently developed the method in practice. There are times when all of us must feel that zoology is much too important and difficult a subject to be left entirely to zoologists.

GENERAL PRINCIPLES OF VERTEBRATE LOCOMOTION

BY

JAMES GRAY

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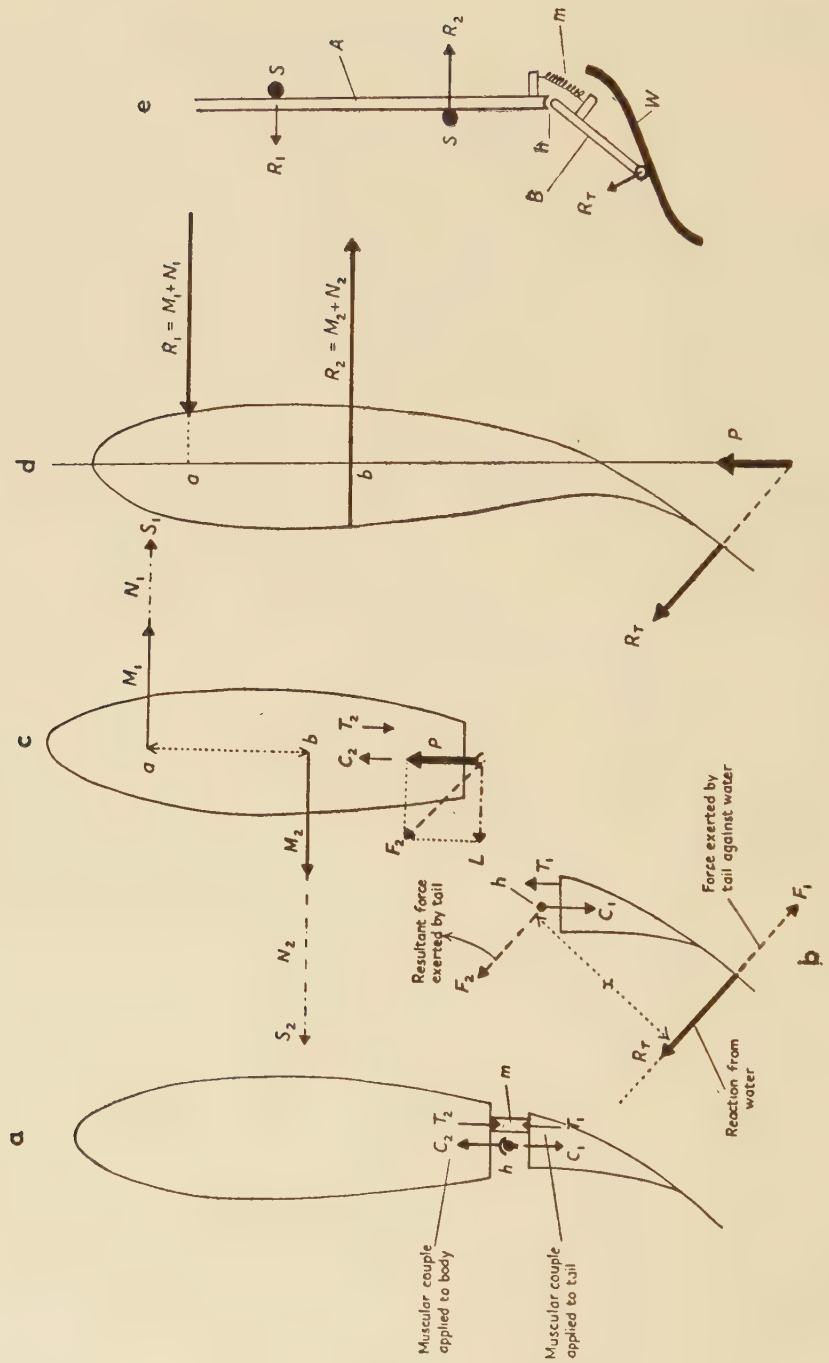
The mechanism whereby the tensile energy of muscles is converted into the useful work of propulsion varies in different types of animal and is characteristically adapted to the particular environment concerned. Only two groups possess locomotory equipment which has—during the course of evolution—become adapted to terrestrial, aquatic and aerial life. These two groups—Arthropods and Vertebrates—are the only ones which utilize the principle of the lever.

The unit of vertebrate propulsion is a pair of bones with muscles operating across their common hinge ; each bone functions as a lever. But, before applying this very familiar concept it is useful to bear in mind two obvious but important facts. (i) When a muscle develops tension it applies equal but opposite forces to each of the two bones. (ii) A muscle cannot develop tension without inducing equal but opposite compression forces between the two surfaces of the joint. The mechanical effect of an active muscle is, therefore, to apply equal but opposite turning couples to each of the two bones. The moment of these couples is determined by the tension of the muscle and the distance between the mechanical axis of the muscle from the centre of rotation of the joint. The plane of action of the couple depends on the position of the points of attachment and origin of the muscles relative to the three main axes of the bones, but for practical purposes the plane of movement of the bones is more conveniently referred to the main axes of the animal's body. In fish the rotations of the vertebrae are effectively restricted to the median transverse plane : in tetrapods, on the other hand, the muscular system is very much more complex and a single muscle may rotate a bone about more than one of the principal axes of the body.

A complete picture of the locomotory activity of any vertebrate would involve a precise knowledge of the changes in length and tension of a very large number of muscles and an accurate knowledge of their anatomical arrangement. In practice, it is exceedingly difficult to obtain this information concerning even one muscle, *in situ*, without interfering with the animal's freedom of movement ; to extend such observations to a large number of muscles would be quite impracticable. A more useful picture emerges by applying the general principle that an animal cannot, by internal muscular effort, apply a propulsive force to its body without exerting an equal backward thrust against the external environment. If the magnitude and direction of this backward thrust can be determined it is possible to calculate the mechanical effort being exerted by the muscles operating about each of the joints of the body. This principle can be applied by making an imaginary section through the joint concerned and considering the moment of all the



Caption on facing page.

external forces acting on each side of the joint. Fig. 1 illustrates the application of the principle to a typical carangiform fish, on the assumption that the only substantial external force acting posteriorly to the vertebral hinge (h) is the reaction (R_τ) of the water against the caudal fin. It is the longitudinal forward component (P) of this reaction which drives the fish forwards. If the front end of the body is to be restrained from oscillating from side to side it must elicit from the water transverse forces (R_1 and R_2) whose moment about the hinge is equal but opposite to that of R_τ ; and the effort of the muscles operating about the hinge is equal but opposite to that of the external forces. In practice, it is difficult to press the argument beyond this point until much more detailed information is available about the distribution of the forces exerted by the water over the whole surface of the fish ; only then, will it be possible to assess the mechanical efficiency of the whole system with any degree of accuracy. Similar and even greater difficulties arise in connection with aerial propulsion.

In terrestrial tetrapods the mechanical problems are very much simpler for in many cases the external forces exerted against the ground are often concentrated at relatively well defined and localised regions of the feet and can therefore be reasonably accurately determined by experimental methods. The body of the animal can be regarded as a horizontal beam supported by four extensible and moveable limbs (Gray 1944). Each limb represents a series of articulated levers with the proximal element articulated to the body. The functions of support and propulsion depend on a high degree of co-ordination of the muscles operating about each of the joints, but before considering the forces which they exert during locomotion it is convenient to consider those which exist whilst the animal is standing at rest.

Fig. 1—Relationship between the force propelling a fish and the forces exerted by the lateral musculature.

a : the muscles (m) on the right side of a vertebral hinge (h) are under tension and are applying a clockwise turning couple (C_2, T_2) to the front end of the body and an equal but opposite couple (C_1, T_1) to the tail and caudal fin. The tail of the fish is moving towards the right side of the body.

b : the pressure (F_1) exerted by the tail against the water elicits the reaction (R_τ) acting normally to the surface of the fin, and the moment ($R_\tau \alpha$) of this force about the hinge is equal to that of the muscular couple (C_1, T_1). The resultant of the couple and the force R_τ is F_2 equal and parallel to R_τ acting at the surface of the hinge against the front end of the body.

c : the force F_2 has two components : one (P) drives the fish forwards, the other (L) tends to rotate the front end of the body and to displace it to the left. The same mechanical effect as L would result from two lateral forces : N_1 acting at a and N_2 acting at b. Similarly, the effect of the muscular couple (C_2, T_2) is equivalent to lateral forces (M_1 and M_2) also acting at a and b. The resultant forces (S_1 and S_2) tend to produce turning and lateral displacements.

d : if the head of the fish is to move forwards without oscillating from side to side, the front end of the body must be subjected to external lateral forces (R_1 and R_2) equal but opposite to S_1 and S_2, the resultant of R_1 and R_2 being equal but opposite to the lateral component (L) of the force (R_τ) exerted by the water against the tail.

e : principle of a working model. The front end of the body is represented by the rod A, the tail and caudal fin by rod B. The muscles are represented by a spring, and the water, pressing against the tail, by a rigid slide (W). The rod A is prevented from lateral displacement by the stops (S). If the spring develops tension the model slides forward.

In Fig. 2a a forelimb is shown with the centre of pressure of the foot vertically below the centre of attachment of the shoulder muscles to the body. The line joining those two points is the mechanical axis of the limb. Under such conditions the only force which the limb can exert against the body acts vertically upwards at the shoulder, and the effort required from each of the intrinsic muscles of the limb depends on the magnitude of this force and on the distance of each intrinsic joint from the mechanical axis : the limb is acting as a vertical strut. In Fig. 2a the hind limb is inclined backwards relative to

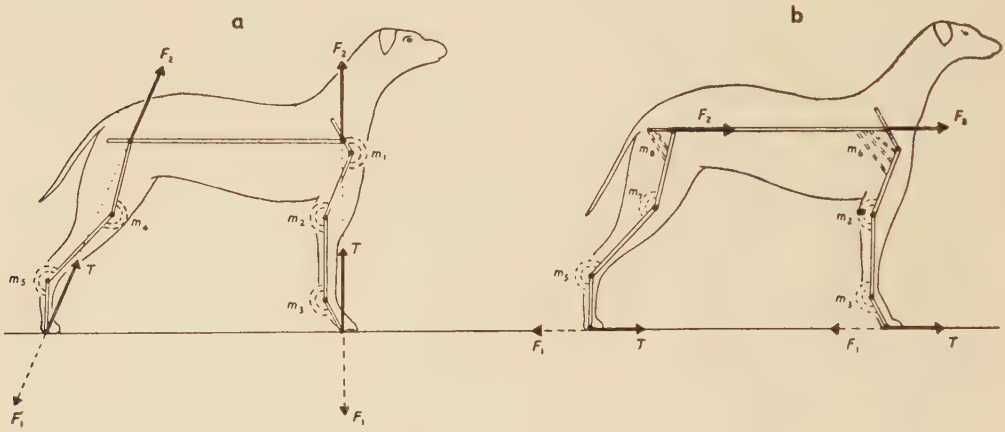


Fig. 2—Mechanical functions of limbs.

a : Both limbs functioning as struts. The equal but opposite forces (F_1, F_2) which the limb exerts against the ground and against the body act along the limb's mechanical axis, i.e. along the line joining the centre of pressure of the foot to the centre of rotation of the joint by which the limb is attached to the body. In the figure the axis of the fore-limb is vertical and only a vertical force is applied to the body ; the hind-limb is inclined and the body receives a forward propulsive thrust as well as a vertical supporting force. The active muscles (m_1–m_5) are shown by dotted lines ; no differential strain falls on the retractor or protractor muscles of the shoulder or hip.

b : Both limbs operating as levers. Couples are developed by the retractor muscles of the shoulder and hip (m_6, m_8). The forward thrust applied to the body is equal to the friction (T) acting against the feet. Note that the activity of the shoulder and hip muscles necessitates appropriate changes in the activity of the intrinsic muscles of the limbs (m_2, m_3, m_5, m_7).

the axis of the body, but as its mechanical axis still passes through the hip joint the limb functions as an inclined strut operated by the muscles of the knee and ankle. A limb can only act as an inclined strut if adequate friction operates the foot ; the limb applies a forward propulsive force to the body equal to the amount of friction acting against the foot. The ability of a limb to act as a strut depends entirely on the coordinated activity of the muscles operating about its intrinsic joints ; these muscles, in short, control the forces which the limb exerts along its own mechanical axis. If this thrust is T then the vertical force exerted against the body is $T \cos \theta$ (where θ is the angle of inclination of the limb) and the horizontal force is $T \sin \theta$.

But, in addition to acting as a strut, the limb as a whole can function as a lever by developing turning couples by means of the extrinsic muscles which

connect the limb to the body. This is illustrated in Fig. 2b where the retractor muscles of both limbs are operating. If the moment of the muscular couple applied across either the hip or the shoulder joint is M the propulsive force (F_2) applied to the body is $\frac{M}{h}$, where h is the height of the shoulders and higher above the ground. It is important to notice that a limb can only act as a lever provided the couples developed by the muscles operating about its intrinsic joints are suitably adjusted. In a moving animal the limbs function simultaneously as struts and as levers and the activity of all the muscles—both intrinsic and extrinsic must be very closely coordinated. It is also useful to note that a limb cannot function as a propulsive lever without applying a pitching couple to the vertebral column tending to raise the shoulders and lower the hips. In general it may be said that it is only by acting as a strut that the limb can control the vertical forces exerted against the body and only by acting as a lever that it can vary and control the horizontal thrust.

Reverting to the concept of the body as a horizontal beam supported by four limbs, it is now possible to consider the patterns of coordination between them when the animal is still standing at rest. For this purpose it is convenient to start (as in Fig. 3a) with the axes of all the limbs vertical and the centre of gravity equidistant from the front and the hind limbs. In order that the body should remain at rest the vertical thrust of the individual limbs must satisfy three equations.

$$T_{LF}+T_{RF}+T_{LH}+T_{RH}=W \quad . \quad . \quad . \quad . \quad . \quad \text{(i)}$$

$$\frac{l}{2}\left(T_{LF}+T_{RH}\right)=\frac{l}{2}\left(T_{LH}+T_{RH}\right) \quad . \quad . \quad . \quad . \quad . \quad \text{(ii)}$$

$$\frac{t}{2}\left(T_{LF}+T_{LH}\right)=\frac{t}{2}\left(T_{RF}+T_{RH}\right) \quad . \quad . \quad . \quad . \quad . \quad \text{(iii)},$$

where W is the weight of the body and T_{LF}, T_{RF}, T_{LH} and T_{RH} are the vertical thrusts of the left fore, right fore, left hind and right hind limbs respectively ; l is the distance between the front and hind feet and t is the distance between the right and left feet. From these equations it can be seen that (for an animal whose centre of gravity is equally distant from the front and hind feet) one half of the total weight must be distributed between the two front and two hind feet respectively ; and one half between the two left feet and between the two right feet. A more significant deduction can be drawn by ascribing a particular value (x) to the vertical thrust of any one limb, thus enabling that of each of the others to be calculated. If the thrust of the left fore limb be x then

$$\text{Right fore limb } (R_F) = \frac{W}{2}-x \quad . \quad . \quad . \quad . \quad . \quad \text{(iv)}$$

$$\text{Left hind limb } (L_H) = \frac{W}{2}-x \quad . \quad . \quad . \quad . \quad . \quad \text{(v)}$$

$$\text{Right hind limb } (R_H) = x \quad . \quad . \quad . \quad . \quad . \quad \text{(vi)}$$

In other words the vertical thrusts of diagonally situated limbs must always be the same ; any increase or decrease in the effort of the left fore limb must be accompanied by a similar change in that of the right hind limb ; at the same

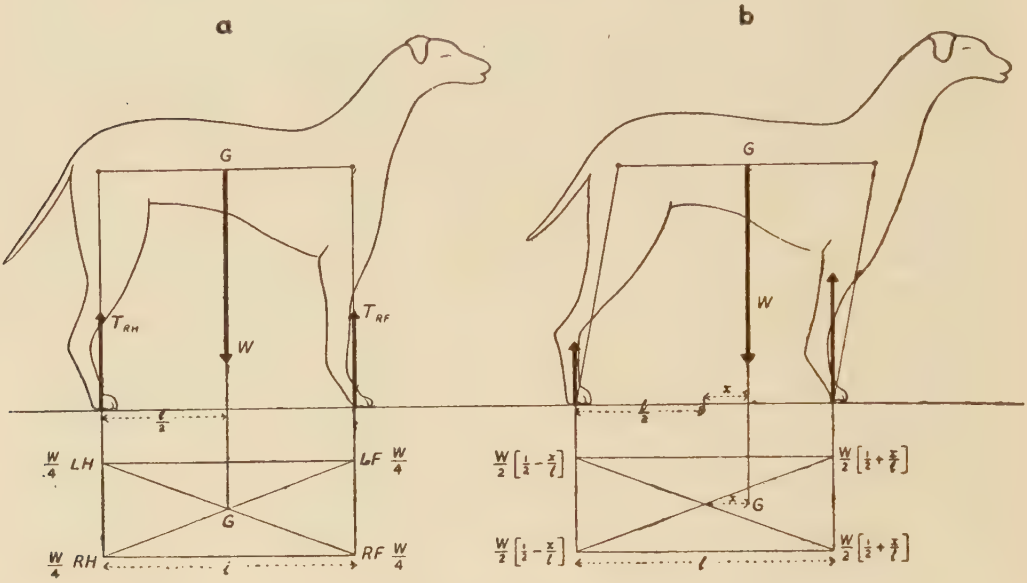


Fig. 3—General principles of support and propulsion of the body.

a : The centre of gravity (G) of the animal shown lies midway between the shoulders and hips ; the limbs are vertical. *If the vertebral column is to be free from all torsional strain,* the vertical forces exerted by each limb in its function as a strut must be the same for all four limbs (LH, RH, LF, RF)—each carrying one-quarter of the total weight of the body (W), as shown in the lower part of the diagram. The centre of gravity of the body is vertically above the intersection of the lines joining diagonal limbs. T_{RH} and T_{RF} are vertical thrusts exerted by the right hind- and right fore-limb respectively, and l is the distance between the front and hind-feet.

b : The animal has moved its shoulders and hips forward through a distance x relative to its feet. To enable the animal to stand in this position, with its back still free from torsion, the limbs must be operated as levers and their vertical thrusts adjusted to the values shown in the figure. The animal can lift either of its hind-feet provided (i) the muscles of the back develop adequate torsional couples ; (ii) the thrust of the diagonal fore-foot is reduced by an amount previously exerted by the lifted hind-foot ; (iii) the thrusts of both limbs of the other diagonal limbs are increased by a corresponding amount. If the left hind-foot is lifted, the thrust of the right fore-limb must become $\frac{W}{2}\left[\frac{2x}{l}\right]$ that of the left fore-limb $\frac{W}{2}$ and that of the right hind-limb $\frac{W}{2}\left[1-\frac{2x}{l}\right]$.

time a corresponding change but of opposite sign must occur in each of the two limbs of the other diagonal. In other words, the well-known " extensor reflex " receives a functional meaning in terms of purely mechanical factors. Equations (iv)–(vi) show that the thrust of any individual limb can vary from $\frac{W}{2}$ to zero without involving instability of the body except at the extremes of this range. On the other hand, unless the weight of the body is equally distributed between each of the four limbs, the vertebral column must actively resist

torsion—the greater the difference between the individual effort of the two front or two hind limbs the greater is the torsional strain falling on the muscles of the back. A comparable pattern of diagonal coordination is also necessary when one member of a diagonal pair operates as a lever and applies a propulsive thrust to the body ; if the left fore limb exerts a horizontal thrust, the right hind limb must exert an equal effort if the body is not to rotate about its median vertical axis.

When an animal is in motion, the vertical and propulsive forces exerted by an individual limb change rhythmically during each cycle of movement, but exactly the same principles apply as to the animal at rest provided the rate of motion is constant and provided the animal can come to rest at any instant without losing stability ; there must always be a well defined pattern of muscular effort spreading throughout the whole of the masculature of the limbs and vertebral column.

As soon as the body of the animal shown in Fig. 3a begins to move forward relative to the feet as in Fig. 3b the centre of gravity of the body, moves forward and lies nearer to the front feet than to the hind ; when it falls within the triangle defined by the two front and one hind foot, the other hind foot can be lifted off the ground and be swung forward. For stable progression, the centre of gravity must always lie within the triangle of the three feet which are on the ground—in other words a hind foot can only be lifted when the centre of gravity lies in front of the line joining the other hind foot to its diagonal fore limb, and a fore limb can only be lifted as long as the centre of gravity lies behind the line joining the other fore limb to its diagonally situated hind limb.

If three feet are always to be on the ground, it follows that during each complete cycle of its movements each limb must be off the ground for one quarter of the cycle and on the ground for three quarters. If, at the same time, the centre of gravity of the body always falls within the triangle of the three feet which are on the ground it follows—from purely geometrical reasons—that the feet must be lifted from the ground in a particular order, viz. LF, RH, RF, LH. This order is usually referred to as the " diagonal sequence " of limb movements and it is highly characteristic of all quadruped animals when walking slowly but steadily ; it is in fact the only pattern of movement in which the body is statically stable at all phases of the walk.

The extent to which these principles give an adequate picture of a slowly moving tetrapod can be tested by allowing a walking animal to place each foot in turn on a balance so designed as to measure the vertical and horizontal forces exerted during its effective cycle. Observations of this type have been made by Manter (1938) in the case of a cat and by Barclay (1946) in the case of a toad. The results of these authors show, as might be expected, that there is always some variation between the total vertical thrust of the limbs and the total weight of the body—and consequently the body rises and falls rhythmically during each complete cycle of movement of the four limbs ; and there may or may not be some tendency for the body to sway from side to side. Apart from these features, the observational data conform closely with the mechanical principles described above.

As the pace of an animal quickens, each foot is lifted slightly before the one next ahead of it in the sequence has reached the ground, and there are phases of movement in which only two limbs are on the ground instead of three. With still greater increase of speed, the periods during which three limbs are on the ground becomes shorter and shorter until eventually only two limbs support and propel the body simultaneously ; usually diagonal limbs work together, as in a trot ; but sometimes, as in a rack, the two ipsilateral limbs collaborate. In the fastest gait—or gallop—the two fore- and two hind-limbs function more or less simultaneously. In all cases, however, the centre of gravity of the body falls during certain phases of progression and has to be raised again when the appropriate foot or feet can again exert active thrusts against the ground.

Starting and checking of movements

Within the limits of this article, it is impossible to consider more than a few general characteristics of the muscular effort involved by the locomotion of an animal such as a horse or of a man, but a few easily observed phenomena illustrate the dominating extent to which the organism adjusts the use of its muscles to conform with relatively simple mechanical principles. In starting from rest, the main effort is against the inertia of the body or of any external load. For example, a horse starting to move a heavy van moves its feet backwards relative to the hip and shoulder joints before applying powerful leverage from the muscles operating about these joints. These phenomena find their explanation from the principle, already mentioned, that the muscles of the hips and shoulders cannot exert their propulsive couples on the limbs without exerting equal but opposite pitching couples on the body—in other words without transferring weight from the front limbs to the hind-limbs. The larger the extent to which the total weight of the body is initially carried by the front feet, the greater is the horizontal propulsive thrust which the limbs can develop ; the forward thrust applied to the body cannot exceed the friction operating at the feet and this depends on the amount of weight which the feet are carrying. The upward tilt of the body in response to powerful contractions of the hip and shoulder muscles can readily be seen when a standing horse is suddenly spurred into motion, the front legs being lifted well off the ground. A similar principle operates when a man starts to sprint from rest ; the hip muscles can enable the legs to exert a powerful propulsive thrust against the ground only if the couple which these muscles exert against the body is able to raise the body from a horizontal to a vertical position ; hence, the sprinter's characteristic starting posture.

When an animal starts from rest, a large fraction of the tensile energy of its muscles is utilized in the useful work of endowing the body with kinetic energy, and so long as the translatory speed is rising some useful work is done. Eventually, a maximum speed is reached and at this point all the energy of the muscles is being dissipated against internal resistances, except the very small fraction required to overcome the resistance of the surrounding air. To some small extent the increase in internal resistance associated with high translatory speeds may be due to increased frictional forces within the muscles

Fig. 4—Phases in the "transverse" gallop of a horse (from Maybridge 1899). Note the flexion of the limbs when they are swinging forward. The hoof is placed on the ground when it is moving backwards relative to the hip or shoulder at the same speed as the body is moving forward relative to the ground.

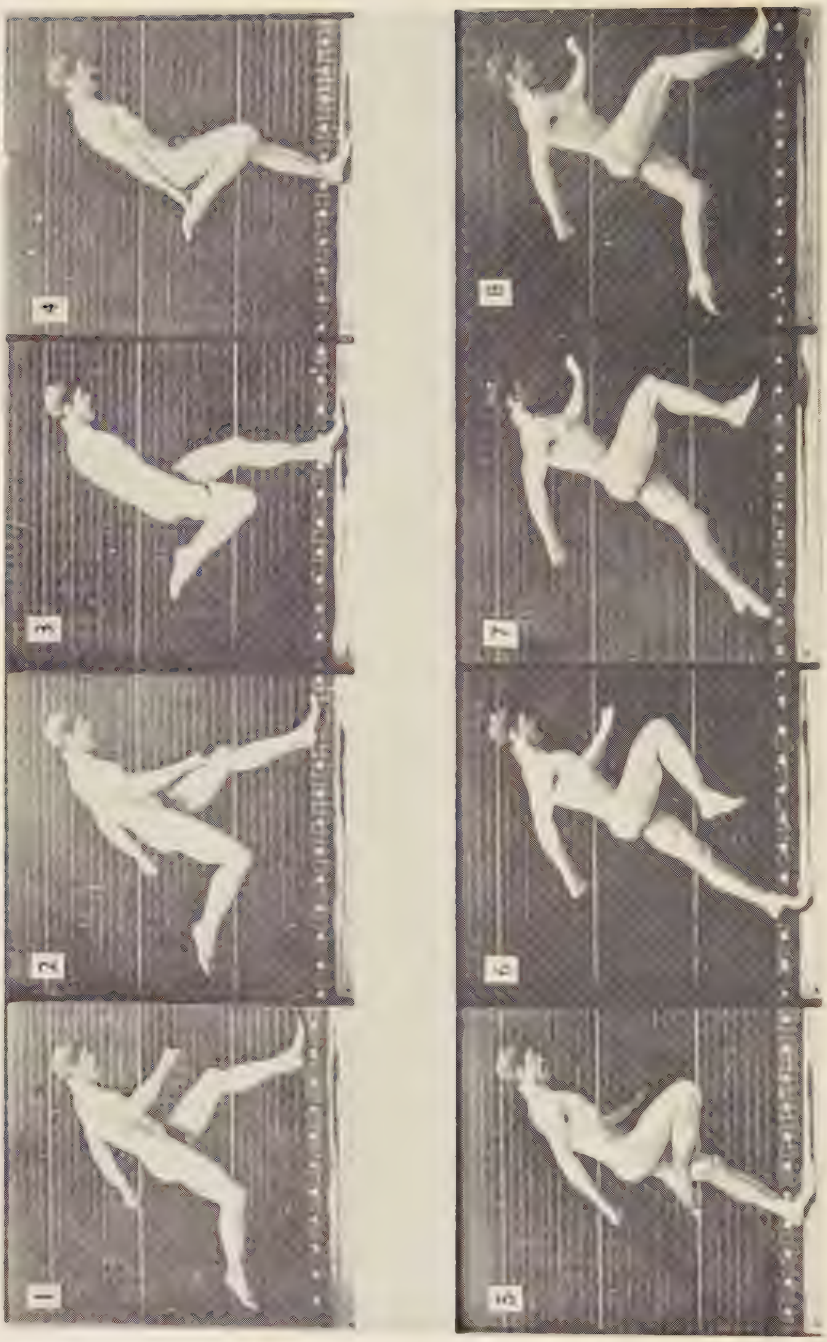


Fig. 5.—Phases of the human limbs when running. Note the flexion of the knee when the leg is moving forward; the foot is placed on the ground when it is nearly under the centre of gravity of the body.

and the joints, but to a very much greater extent it is due to the inertia of the limbs themselves which must be kept moving relative to the body. For example, when a horse is running steadily at 30 miles per hour, the horizontal forces exerted by the feet against the ground are negligibly small compared with those operating when the speed is rising relatively rapidly. In a steadily moving animal the main function of the limbs is to prevent the body falling under gravity ; in fulfilling this role they do very little useful propulsive work but they consume a very considerable amount of energy. The movement of the limbs of a running horse is illustrated by Fig. 4. This figure shows that, although a limb is fully protracted at the end of its forward swing, it does not establish contact with the ground until the hoof is nearly vertically below the hip or shoulder ; at this stage the hoof is travelling backwards relative to the hip or shoulder at the same speed as the body is travelling forwards relative to the ground ; in other words, at the moment of contact the hoof is stationary relative to the ground and can exert a vertical thrust without eliciting any frictional resistance from it. In order to establish these conditions, the force applied by the retractor muscles to the fully extended limb must be such as will give the limb sufficient acceleration to raise the speed of the hoof to 30 miles per hour within a distance equal to about one-half of the limb's natural swing. A rough estimate of the acceleration required is about six times that of gravity. During the whole period of contact with the ground the foot must continue to move backwards relative to the body with unreduced speed ; Fig. 5 shows that the backward movement of the limb continues after the hoof leaves the ground. To check the backward swing of a limb before the hoof has left the ground would operate the limb as a brake ; to check it immediately after it leaves the ground would involve an intense effort by the protractor muscles just before they are being called upon to swing the limb forward. In practice the horse allows its limb to complete its backward swing after the foot has left the ground on the same principle as the club and shoulders of a golfer " follow through " after the ball has been struck ; in both cases the danger of checking the speed of the limb or club too soon is avoided. As soon as the limb has come to rest in the fully retracted position it has to be swung forward again ready for the next step. The speed at which the protractor muscles can accomplish this depends on the moment of inertia of the limb. Fig. 4 shows how the work of the protractor muscles is minimized by sharp flexure of the limb and consequential reduction of its moment of inertia. Precisely similar phenomena are noticeable in human running (Fig. 5). It would be interesting to know how far the difference between an expert and an indifferent athlete depends on the possession of more powerful muscles and how far on the conscious or unconscious ability to use his muscular energy to its best physical advantage.

REFERENCES

Barclay, O. R. (1946). The mechanics of amphibian locomotion. *J. exp. Biol.* **23** : 177–203.
Gray, J. (1944). Studies in the mechanics of the tetrapod skeleton. *J. exp. Biol.* **20** : 88–116.
Manter, J. T. (1938). The dynamics of quadrupedal walking. *J. exp. Biol.* **15** : 522–540.
Maybridge, E. (1899). *Animals in motion.* London.

PROBLEMS OF FISH LOCOMOTION

BY

RICHARD BAINBRIDGE

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The main problems still outstanding in the field of fish locomotion are considered in turn. One of these, concerning power and drag, is treated at greater length. Formulae are developed showing a theoretical relationship between speed, weight of muscle, a power factor and length, for a hypothetical fish. These calculated speeds are then compared with various old and newly measured speeds and the discrepancies discussed. It is concluded that there is no problem with smaller fish and large whales, but forms of intermediate size do show some anomalies. It is considered that, except for the barracuda, these may most easily be accounted for by attributing a higher power factor to the muscles of these organisms, although abnormal hydrodynamical conditions may still be of some consequence.

CONTENTS

	Page
Introduction	13
The precise form of movement of the body and caudal fin	14
The nature of the flow pattern over the surface of the body and and the tail fin	14
Evaluation of the drag at the surface of the swimming fish	15
The efficiency of undulatory movement in imparting energy to the water	16
The significance of exhaled water	16
The relationship of body and tail form to habit	17
Considerations of power and drag in fish locomotion	18
(*a*) Derivation of the formulae relating necessary power to available power	18
(*b*) Evaluation of the factors involved	20
(*c*) Calculation of expected velocities	22
(*d*) Graphical representation	24
(*e*) Conclusions	27
Summary	28
Acknowledgments	29
References	29
Appendix	30
General discussion	31

INTRODUCTION

Despite the great amount of work devoted to the locomotion of fish in the past sixty or seventy years there remain many outstanding problems both of intriguing interest and with potentialities for practical application. It is my intention first to survey the major groups of these problems briefly and then to consider one of them in greater detail in the light of recent measurements on the abilities of smaller fresh water fish. It would seem reasonable to list the outstanding topics in seven major categories :

THE PRECISE FORM OF MOVEMENT OF THE BODY AND CAUDAL FIN

Since Breder (1926) first distinguished three types of movement (Ostraciiform, Carangiform and Anguilliform) on the part of fish propelled by lateral undulations of the body it seems to have been widely assumed that these are clear cut categories. Although the two extremes of Ostraciiform and Anguilliform movement are quite distinct it would in fact seem most reasonable to regard them as the limits of an intergrading series of fish showing combinations of these two types of movement in different degrees.

Any mathematical analysis of the thrust that might be expected from an undulating surface in water is dependent upon an accurate knowledge of the movement of that surface. Ostraciiform and, particularly, Anguilliform movement, although complex enough, have shown themselves amenable to such mathematical study, Gray (1933 a), Gadd (1952) and Taylor (1952). What, in the intermediate series, might be termed the more ostraciiform Carangiform swimmers have also proved simple enough to be treated similarly, Gero (1952). Many of the fast swimming oceanic scombroids fall into this category, as the propulsive thrust here seems to come largely from a tail fin of high aspect ratio moved at the end of a fairly narrow peduncle ; it being assumed that little thrust derives from the rather limited movements of the most posterior part of the body proper. The dolphins, porpoises and whales fall into this category too, despite their dorsoventral movements. Parry (1949) has shown it possible to reach reasonable estimates of the thrust developed by these forms on a consideration of the movement of the tail flukes alone.

The more anguilliform of the Carangiform swimmers present a problem of another order however and it is into this category that most of our common fresh-water fish fall. We already have some idea of the frequency, amplitude and wave length of the more posterior parts of the body and of the relationship of these to the size and velocity of the fish, Bainbridge (1958 a). The relative contributions of the body itself, particularly of the deep caudal peduncle and of the tail fin, to the total thrust are however not readily determinable, Gray (1933 b). Observations of the movement of the tail fin further shows this to involve complex bending in both a vertical and a horizontal plane, Bainbridge (1958 b). This is coupled with a regular increase and decrease in area at different positions in the cycle of beating that would seem to imply an active use of the intrinsic fin ray muscles. Clearly any mathematical analysis of the possible thrust from so complex a moving surface is dependent upon a most accurate description of the form of these movements. This is so far lacking but attempts are at present being made in Cambridge to provide such a description. In particular the varying angle of attack of different parts of the tail at different positions in the cycle is now being successfully measured.

THE NATURE OF THE FLOW PATTERN OVER THE SURFACE OF THE BODY AND THE TAIL FIN

Considering the importance attached to the nature of the flow over the body surface by all who have made any attempt to draw up a balance sheet between the power available and the power necessary for fish locomotion, it is

perhaps surprising that a greater effort has not been directed towards solving this particular problem. The practical difficulties involved may to a certain extent account for this.

Gray and Lissmann (unpublished) have made attempts using the optical properties of tobacco mosaic virus in polarised light, and Rosen (1959) refers to a new method that he claims has produced striking results. The desirability of some precise information in this field can hardly be overstressed. The clear demonstration of either laminar or turbulent flow over the surface of an actively swimming fish, the position of the boundary, if one exists, between these two regions and some assessment of the energy wasted in producing eddies and vortices would all assist in our understanding of fish locomotion. The influence of the frequently encountered highly flexible trailing edge upon separation of flow and the production of a Karman vortex trail could also profitably be studied. Both Gero (1952) and Lighthill (1960) emphasise the importance of the way in which this posterior surface of the fish sheds energy.

EVALUATION OF THE DRAG AT THE SURFACE OF THE SWIMMING FISH

Measurements of the drag of anaesthetised fish are relatively easy to make by timing their rate of fall in a tall column of water. Magnan (1930) and Magnan & Saint-Lague (1930) give the first recorded measurements derived by this technique and it has since been followed by Richardson (1936), Gero (1952) and Bainbridge (unpublished). Gero gives an account of techniques and calculations in great detail without including any results. But he does state that these confirm those of Richardson. Fish or models of fish have been towed in water, Houssay (1912), Kempf & Neu (1932) or held by a measuring balance in a water channel, Bainbridge (unpublished). Magnan & Saint-Lague (1929) and Gray (1957) have also made drag calculations for fish photographed while gliding passively to rest after a period of swimming.

The clear deduction from these various measurements is that the drag of such passive fish bodies is as would be expected on ordinary hydrodynamical grounds and that the flow pattern must be largely laminar at the low Reynolds numbers involved. It further seems that the nature of the surface, whether rough or smooth or coated with mucus, has little influence on the total drag. This is also in accordance with expectation on hydrodynamical grounds. Such findings have led to a general acceptance of the belief that reasonably accurate estimates of the drag of any passive fish can be reached by treating it as a simple three dimensional body of rotation and applying the appropriate hydrodynamical formulae.

Evaluation of the drag produced by the surface of an *actively swimming* fish is a much more difficult task. Gero (1952) proposes calculations in which friction and form coefficients are used for the more anterior parts of the body not producing thrust and an induced drag coefficient for the posterior, propulsive parts. Lighthill (1960), considering the propulsive effect of the entire length of a hypothetical slender fish making swimming movements only in a single direction at right angles to its direction of locomotion, takes account of both the frictional drag and the lift and drag forces arising from the

lateral movements and the effect of separation and vortex shedding. The thrust derived in this way (and already including drag components) is then equated to the standard drag formula for a passive body. But his complex theoretical formulae do not readily lend themselves to substitution without much more accurate knowledge of the exact form of movement of the fish involved.

THE EFFICIENCY OF UNDULATORY MOVEMENT IN IMPARTING ENERGY TO THE WATER

There are so many unknown or only partially known factors concerned in the locomotion of fish that it is not possible to make any assessment of the external efficiency of the propulsive mechanism by drawing up a balance sheet for the whole system. Indeed some assumption of this degree of efficiency must be made before it is possible to make such a balance sheet. Measurements of the efficiency of rotating propellers in imparting energy to the water, e.g. Rouse (1946), may be used as an analogy. The maximum efficiency of a well designed propeller is of the order of 75 per cent to 80 per cent. It seems reasonable to suppose that surfaces moving as they do in a fish would have the same order of efficiency.

Gero (1952), Gadd (1952), Taylor (1952) and Lighthill (1960) all make some consideration of the concept of efficiency in their calculations of thrust. Gero uses efficiency as one of his variables and combines it with various power loading parameters to produce different velocities. Gadd defines an " ideal efficiency " measured by the difference between the rate at which the propulsive wave passes down the body and the rate at which the body moves forward. Taylor gives the mathematical conditions governing the relationship between amplitude, velocity and work in a long uniform body propogating a wave of uniform amplitude ; and Lighthill shows that a wave of increasing amplitude from zero at the head to a maximum at the tail is more effective than one of uniform amplitude. He also demonstrates that the wave should pass down the body at a speed of around 5/4 of the desired swimming speed. A measure of the efficiency could, he says, be made by using an extensive computing programme. He gives no clear indication of what the expected answer might be but supposes a value of 0·9 would be too optimistic. He is nevertheless of the opinion that the type of movement found in most fish has a " good efficiency ". It must be remembered that his calculations relate to a hypothetically simplified fish.

It is not immediately apparent how the problem of efficiency in this part of the propulsive system could best be tackled. It must nonetheless be borne in mind as a relevant factor in wider considerations of power and velocity.

THE SIGNIFICANCE OF EXHALED WATER

There seem to be three possibilities relating to the significance in fish locomotion of water exhaled from the gills during respiration. First it may act as a propellent by virtue of its reactive energy ; second it may assist in reducing the drag of the fish surface over which it flows ; or third, it may be of no consequence whatever.

Various factors should be borne in mind in considering the relative likelihood of these three possibilities. In particular : (*a*) the small volume of expelled water in most fish would seem to militate against its use as an active propellent. Hughes and Shelton (1958) give the figure of 40 cc. per min. at a mean head of 0·5 cm. of water as the average output of a 100 gm. trout. Assuming the normal passive drag of the fish body it may be calculated that this volume would only propel it at a velocity of 0·3 cm. per sec. The output would be somewhat higher during more active breathing but not excessively so. (*b*) The relatively small amount of branchial musculature compared with trunk musculature in most fish further implies the unimportance of the former in locomotion. (*c*) Many of the fastest oceanic scombroid swimmers dispense with pumping mechanisms entirely and the respiratory current over the gills is a passive one induced by swimming with the mouth open.

Breder (1924) concludes that the propellent effect of exhaled water may be important in some fish, such as the globefish, *Chilomycterus*. He is of the opinion however that generally its greatest significance must be confined to a reduction of frictional drag by the sheath of exhaled water flowing over the body. In this respect he refers to the work of Paxton on the propulsion of ships by a similar method. This supposed reduction of drag could of course itself increase the importance of the reactive effect of the expelled water.

The contribution to the total drag of the swimming fish by separation of the boundary layer is unknown but it is conceivable that exhaled water could delay the onset of such separation. This, however, is not exactly Breder's original contention. The swimming of scombroids with open mouths also raises the possibility of the partially open opercular covers stabilizing flow over the trunk of the fish in a manner analagous to slotted wings.

It would seem clear that exhaled water alone can be of little importance as an active propellent. The other matters, relating to drag reduction could well be examined more closely however.

THE RELATIONSHIP OF BODY AND TAIL FORM TO HABIT

Harris (1936, 1937, and 1953), has examined fully the mechanical influence of particularly the paired fin pattern and movement on stability in the swimming fish and more generally the influence of this and tail structure on mode of life and habit. Nursall (1958) has considered the aspect ratio of the tail fin and its possible influence on locomotory capabilities and Breder (1926) has also surveyed these problems in a general way.

There seems much still to be done before we have a really full understanding of the whole complex of structural and physiological features that contribute to the different types of successful fish known today. For example, the essential differences between fast and slow swimmers both from a structural, physiological and hydrodynamical point of view are not yet really understood. Nor are the differences between hunters and herbivores or between fish able to sustain high speeds continuously, high or higher speeds for a short burst and high speeds not at all. The partial emargination of the tail in so many of our own fresh-water fish is further both difficult to understand hydrodynamically and difficult to correlate precisely with habit.

CONSIDERATIONS OF POWER AND DRAG IN FISH LOCOMOTION

Houssay (1912) made attempts to record the propulsive power of swimming fish experimentally and Denil (1937) developed similar but more refined methods. Gero (1952) has also made power measurements using an attached line incorporating a strain gauge. Any such study of an actively moving fish is unfortunately only able to indicate the surplus power above that being used by the specimen in moving its body through the water. There appear to be two ways in which the theoretical relationships of power, drag and speed may be considered. Either the hypothetical thrust derivable from the moving body surface may be calculated and equated to the calculated drag to give a value for velocity *or* the potential muscle power may be calculated and similarly equated to the drag.

The first of these methods, as already mentioned, necessitates a precise knowledge of the form of movement of the body followed by a most complex mathematical treatment. This approach has been adopted by Parry (1949) for dolphins, by Gero (1952) for large fish, by Lighthill (1960) for a hypothetical fish with simplified carangiform movement and by Gadd (1952) and Taylor (1952) for a hypothetical long narrow body showing an anguilliform type of movement. The relative simplicity of the movement analysed by Parry and by Gero allowed of some direct practical applications. The complexity of the movement analysed by Taylor and by Lighthill on the other hand, leads to mathematics of such rarefied complexity as to make practical application difficult.

Gray (1936) first tackled the problem by the second method of comparing the theoretical power output of the body musculature with the theoretical drag of the body surface. This he did for a dolphin and a porpoise, producing somewhat anomalous results indicating, in his opinion, an ability on the part of the animal to preserve laminar flow over the greater part of the body surface. Having now, Bainbridge (1958), some accurate figures for the speeds of swimming of smaller fish it seems desirable to adopt a similar approach in order to draw up a balance sheet concerning their locomotion and perhaps assess the accuracy of the technique or the efficiency of the propulsive mechanism. While the method of calculation is basically that used by Gray (1936) it differs in certain details as will be indicated.

(a) *Derivation of the formulae relating necessary power to available power*

The standard hydrodynamical formula giving the drag of a surface is :

$$\text{Drag} = \tfrac{1}{2}\rho A V^2 C_f \quad . \quad . \quad . \quad . \quad (1)$$

where ρ is the density of the water, A the surface area, V the velocity of movement and C_f the coefficient of frictional drag. This is the formula which Gray (1936) equated to power available. The drag of a three dimensional body such as a fish is however greater than that calculated merely for its *surface area* because of a second component the *form* or *pressure* drag. This derives from the necessity to displace water during forward movement and is determined in magnitude by the form of the body, specifically its *Fineness Ratio* : the length divided by the mean of the height and width of the body.

Hoerner (1958) shows that a drag coefficient based on surface area but including a component for form drag may be calculated from the relationship :

$$C_{D\,wet}/C_f = 1 + 1{\cdot}5\left(\frac{d}{l}\right)^{3/2} + 7\left(\frac{d}{l}\right)^{3} \quad . \quad . \quad . \quad . \quad (2)$$

Where d is the diameter (or the mean of the height and the width) and l is the length of the body. The proportions of length, height and width vary among the animals we are considering. Some of these figures are expressed as Fineness Ratios in Bainbridge (1960). This variability however has no great effect on the relationship in (2) because of the powers to which the terms are raised. Substitution for a variety of specimens gives a mean value for the new inclusive drag coefficient of $1{\cdot}2\,C_f$. This agrees well with the result of similar arguments by Gero (1952), giving a modified coefficient of $1{\cdot}22\,C_f$ including form drag and an induced drag for the moving tail, all at high Reynolds numbers. The factor 1·2 is therefore introduced into equation 1 to give :

$$\text{Drag} = \tfrac{1}{2}\rho A V^2\, 1{\cdot}2\, C_f \quad . \quad . \quad . \quad . \quad (3)$$

and this is a refinement not included by Gray (1936).

The power necessary to propel such a fish at the velocity V is this drag times the velocity, giving :

$$\text{POWER NECESSARY} = \tfrac{1}{2}\rho A\, V^3\, 1{\cdot}2\, C_f \quad . \quad . \quad . \quad (4)$$

The power available to perform this work may be designated by $P.W_m$, where P is a power factor relating to a unit weight of muscle and W_m is the weight of the propulsive musculature of the fish. This is the expression used by Gray. In choosing values for these two factors he used the total weight of propulsive muscle in the fish and a power factor derived from work done by the total muscle weight of a rowing crew. While the fish is swimming only half the musculature is contracting at any one time. It would therefore seem better to consider the power output of only this half and to use with it a suitable power factor (*vid. inf.*) arrived at by considering both contraction and relaxation in the subject giving the work data. The power available is therefore now represented by :

$$\text{POWER AVAILABLE} = \frac{P.\,W_m}{2} \quad . \quad . \quad . \quad (5)$$

Equations (4) and (5) can only be directly equated if one assumes the mechanical efficiency of the propulsive system in imparting energy to the water to be 100 per cent. In the absence of information to the contrary this seemed a reasonable procedure in Gray's treatment. We have already remarked how little is known of this aspect of fish locomotion. In the light of those remarks however (p. 16) it seems more reasonable to assume that the efficiency would be of the same order as a well designed propeller, i.e. 75 per cent. (4) and (5) are therefore equated on the assumption that 25 per cent of the power is lost in transference to the water :

$$\therefore \tfrac{1}{2}\rho A\, V^3\, 1{\cdot}2\, C_f = \tfrac{3}{4}\, P.\, \frac{W_m}{2} \quad . \quad . \quad . \quad . \quad (6)$$

One other factor may be substituted to simplify this relationship somewhat. Gray (1939) and Parry (1949) give figures relating surface area to length.

A reasonable mean for the fish being considered seems to be $A=0{\cdot}4\ L^2$. Substitution is accordingly made and a re-arrangement then gives :

$$0{\cdot}64\ L^2\ V^3\ C_f = P\ W_m \quad . \quad . \quad . \quad . \quad (7)$$

The two extremes at which this relationship will pertain are set by the values of C_f for, respectively, laminar flow at the upper limit and turbulent flow at the lower. Various formulae are available to express the value of this coefficient under these two conditions. Two have been selected that relate it to the Reynolds number of the body and simplify substitution to a certain extent. They are given by Rouse (1946) :

$$C_{f\ \text{Laminar}} = 1{\cdot}328\ R^{-1/2} \text{ and } C_{f\ \text{Turbulent}} = 0{\cdot}074\ R^{-1/5} \quad . \quad . \quad (8)$$

Reynolds number is expressed by $R=\dfrac{LV}{\nu}$ where L is the length of the body, V the velocity and ν the kinematic viscosity of the water.

The two formulae in (8) thus give :

$$C_{f\ \text{Lam.}} = \frac{1{\cdot}328\nu^{1/2}}{L^{1/2}\ V^{1/2}} \text{ and } C_{f\ \text{Turb.}} = \frac{0{\cdot}074\nu^{1/5}}{L^{1/5} V^{1/5}}$$

Finally, substitution of these two in equation (7), followed by a rearrangement gives two expressions for the expected velocity of the fish, in terms of length, muscle weight and the power factor, with on the one hand fully laminar flow and on the other fully turbulent flow :

$$V_{\text{Lam.}} = \left[\frac{P\ W_m}{0{\cdot}085\ L^{3/2}}\right]^{2/5} \quad . \quad . \quad . \quad (9)$$

and

$$V_{\text{Turb.}} = \left[\frac{P\ W_m}{0{\cdot}01885\ L^{9/5}}\right]^{5/14} \quad . \quad . \quad . \quad (10)$$

(b) *Evaluation of the factors involved*

There are four variables included in equations (9) and (10) and we may briefly consider the values that should be accorded them.

1. The two possible drag coefficients incorporated will indicate the maximum velocity to be expected if the flow is fully laminar on the one hand or turbulent on the other. It is most likely that with fish of the Reynolds numbers to be considered, Bainbridge (1958), the flow will be completely laminar. With increasing size and speed however flow over the anterior part of the body will remain laminar but the remainder will become turbulent. The position of the boundary between the two areas is not readily determinable in an active fish. The inference is however that the expected speed should lie somewhere between that derived from the two formulae, in a position dependent upon the percentage of the surface area still retaining laminar flow.

2. The length of the specimen seems to be the only really amenable variable in the whole argument. It is measured, in the specimens concerned, from the tip of the snout to the most posterior part of the extended tail fin.

3. The weight of the propulsive musculature was determined as in Bainbridge (1960) by dissection and weighing, or is taken from other published results for the larger fish and mammals.

4. The value accorded the Power Factor, P, requires more careful consideration. Gray (1936) used the value of 0·01 h.p./lb of muscle, calculated from figures in Henderson & Haggard (1925) of an output of 2,580 kg.m./min. sustained for 22 min. by an average 150 lb. man in a rowing crew. The value is derived by supposing the man to have $\frac{1}{3}$ of his weight as muscle doing the active work. Parry (1949) cites this same figure in his discussions and shows that for shorter periods of activity an output of more than twice this may be obtained (*ex* Dickinson (1928) and measured with a bicycle ergometer) but he considers it unlikely that whales develop more power than man without going into oxygen debt. Gero (1952) on the basis of his speed measurements on the barracuda supposes all these values to be excessively low and claims that a power output of something like 20 times the Henderson & Haggard figure is needed to account for the performance of this fish.

In the light of these various opinions it seemed desirable to collect together and consider the available figures for the power output of different muscles. Table 1 shows ten such values derived from various observations. The output is expressed in terms of ergs per second per gram of muscle as this is the convenient form for substitution in equations (9) and (10). The first three

Table 1—Power output of various muscles.

Species	Period	P(ergs/sec/gm. muscle)	$t°$ C.	Authority
Oryctes	5 min.	3×10^5	25–30	Machin and Pringle
Bombus	5 min.	6×10^5	25–30	Machin and Pringle
Schistocerca	Continuous	9×10^5	30	Weis-Fogh
Canis	7½ min.	$15{\cdot}5\times10^5$	40	Dill, Edwards and Talbott
Canis	10 min.	$1{\cdot}2\times10^5$	38	Taylor
Canis	17 hrs.	$7{\cdot}9\times10^5$	40	Dill, Edwards and Talbott
Homo	22 min.	$2{\cdot}1\times10^5$	38	Henderson and Haggard
Rana	Repetitive contractions	$4{\cdot}0\times10^5$	10	Hill
Rana	Repetitive contractions	17×10^5	30	Hill
Rana	Repetitive contractions	42×10^5	40	Hill

entries, for insects, are from Machin & Pringle (1959) ; the next four, for dog and man, have been calculated from figures in Henderson & Haggard (1925), Dill, Edwards & Talbott (1933) and Taylor (1957). These calculations are based on the assumption that 40 per cent of man's weight is propulsive muscle and 50 per cent of the dog's weight is, while in both cases $\frac{3}{4}$ of the musculature is supposed to give the forward propulsive thrust, while the remaining $\frac{1}{4}$ returns the limbs to their original position during relaxation of the former part. Latimer (1944) gives three figures for the average percentage weight of musculature in man and Dursy (1863) gives three other figures, the mean of all these being 40 per cent. Latimer also gives an average percentage weight for musculature in cats as 50 per cent. No dog figures seem readily available. The three frog values were kindly derived for me from Hill's (1939) data by Dr K. E. Machin. They relate to repetitive contractions of an isolated frog sartorious muscle and the method is described in the appendix.

The value in the Table of $2{\cdot}1\times10^5$ for man corresponds to Gray's figure of 0·01 h.p./lb. of muscle. It differs in being adjusted by the factor $\frac{3}{4}$ (*vid. sup.*) ; and thus relates to a single contraction. This value is therefore properly

applied to the fish when the total weight of fish muscle is divided by two as in our formulae. It should then give a more accurate estimate of the output of the fish muscle than Gray's direct comparison between the total weight of fish muscle and the total weight of human muscle.

Appreciation of the very different abilities of fish when they are swimming in a sustained manner and when they are only indulging in a sudden burst, Bainbridge (1960), makes it desirable that two power output values be considered. The first, appropriate to bursts of swimming, is perhaps determined by the strength and mechanics of the muscle. The second, appropriate to sustained swimming, is perhaps controlled by the arterial supply and respiratory system as a whole. The absolute maximum for a burst of swimming might be indicated by the frog calculation. In this case it would not be unfounded to assume outputs of say :

Fish in cold water	8×10^5 ergs/cm./gm. of muscle
Fish in tropical water ..	17×10^5 „ „ „ „
Mammal	42×10^5 „ „ „ „

The ability to sustain such an output, depending perhaps upon body size and the nature of the circulatory system, is probably very variable. This factor may account for the large differences in Table 1 between say, the dog and the man figures. It is only possible to make some intuitive sort of guess concerning the values for a sustained output and the following have therefore been arbitrarily chosen :

Fish in cold water	2×10^5 ergs/cm./gm. of muscle
Fish in tropical water ..	4×10^5 „ „ „ „
Mammal	4×10^5 „ „ „ „

(c) *Calculation of expected velocities*

Formulae (9) and (10) have thus been used, with a value for P of 2×10^5, to calculate the expected speeds of five fish ranging in size from 10 cm. to 30 cm., the measured speed of which is recorded in Bainbridge (1960). The calculated values for completely laminar and completely turbulent flow and the measured values for both bursts of swimming and sustained swimming are given in Table 2, together with the measured propulsive muscle expressed

Table 2—Calculated and measured speeds of various small fresh water fish.

Species	L (cms.)	Calculated speed (L/sec.)		Measured speed (L/sec.)		Muscle as percentage body weight
		Laminar	Turbulent	Burst	Sustained	
Dace	10·0	18·7	14·3	13·2	4·4	61
Dace	15·0	13·3	9·7	11·7	4·7	56
Goldfish	15·0	15·7	11·2	10·0	3·0	45
Trout	15·6	15·1	10·7	10·7	5·2	63
Trout	30·0	11·4	7·3	10·7	2·6	63

as a percentage of the body weight. The speeds are expressed in body lengths per second to facilitate comparison. It is at once apparent that the measured sustained speeds are well within the expected range even if the flow is completely turbulent. The measured bursts of the 10 cm. dace, the goldfish and

the 15·6 cm. trout are also below the calculated turbulent velocities. Only the 15 cm. dace and the 30 cm. trout would need either the higher (burst) power factor of 4×10^5, or some laminar flow, to bring them into the expected range. Yet the Reynolds numbers of all these fish at even their maximum speeds suggests that the surface flow will be completely laminar.

If the reliability of the measured speeds is accepted and the techniques involved, Bainbridge & Brown (1958), point to such reliability, then there appears to be no problem whatever associated with the locomotion of such small fish. Indeed it might be wondered why they do not manage to effect greater speeds than those recorded.

It is now perhaps of some interest to use the present formulae to examine the data in which earlier authors, Gray (1936), Gero (1952), have found discrepancies. The results of such substitutions for a barracuda, Gero (1952), a porpoise and a dolphin, Gray (1936), and a whale, Hill (1950), are therefore shown in Table 3. Only one set of measured speeds is recorded in this table.

Table 3—Calculated and measured speeds of larger swimming organisms.

Species	L (cms.)	Calculated speed (L/sec.)		Measured speed (L/sec.)	Muscle as percentage body weight
		Laminar	Turbulent		
Barracuda	122	4·3	2·3	10·0	20
Porpoise	122	5·9	2·9	6·2	13
Dolphin	173	5·7	2·8	5·5	17
Whale	2,560	1·7	0·5	0·3	40

There is no indication as to whether these are for bursts of swimming or whether they can be sustained. Three of the specimens listed are warm blooded and the barracuda is a tropical fish. Brett (1956) surveys the effect of temperature on the activity of fish and Fry & Hart (1948) and Brett, Hollands & Alderice (1958) have shown how cruising speed can vary with water temperature. The maximum sustained cruising speed occurs at a particular water temperature in particular fish. Higher temperatures give reduced activity and are finally lethal. Oosten (1957) reports that such large active swimmers as the tunny may have a body temperature 6° to 12° C. above that of the environment. The power factor used for all these calculations is therefore 4×10^5.

Examination of Table 3 reveals the greatest discrepancy for the barracuda, with a measured velocity more than double the calculated one for completely laminar flow. The porpoise and dolphin give a reasonable correspondence, should the flow be completely laminar, while the whale should be able to accomplish his measured speed with great facility even if the flow were completely turbulent. Findings of previous workers are thus confirmed in this respect.

Gray (1936) was of the opinion that the porpoise and dolphin problem was most readily settled by supposing the flow over the surface to be completely laminar. It is still not clear how such flow could be maintained, but work by Kramer (1960 a & b) shows that particularly resilient surfaces can reduce their drag to something about half way between the fully turbulent and fully laminar coefficients. He further maintains that the nature of the dolphin

skin is such that it could produce this type of effect. But there is no experimental evidence that such a surface can induce completely laminar flow. The alternative explanation, that the power factor used is too low, should thus perhaps be reconsidered in the light of the figures in Table 1. The arbitrary choice of 4×10^5 for a sustained output may be wide of the mark ; a figure of 8 or even 16×10^5 would not be impossible. Further we do not know how long these speeds are maintained by the dolphin, although there are indications that it is for considerable periods. It is therefore possible that a burst coefficient of say 32×10^5 should be used. An indication of the power factor necessary to obtain the measured speed can be obtained by substituting this speed in formulae (9) and (10). When this is done for the porpoise a value of $4{\cdot}5\times10^5$ is found to give the right velocity with completely laminar flow, and one of $30{\cdot}8\times10^5$ with completely turbulent flow. Even the second of these values is not out of reason for a short burst of swimming. With part of the flow laminar and part turbulent a power factor of say 16×10^5 could readily account for the observed speed without extraordinary hydrodynamical conditions.

The behaviour of the barracuda poses a greater problem. If the reverse calculation is done with this specimen it is found that a power factor of $32{\cdot}7\times10^5$ is required to account for the measured speed even if the flow is completely laminar. With the flow completely turbulent a figure of 247×10^5 would be required. The latter is certainly out of the question and even the former is somewhat doubtful. There can, I think, be little doubt that this measured speed was only a short burst of swimming. As such it corresponds to the values of about 10 L measured for smaller fish and given in Table 2. One does not doubt that the barracuda is a rapid swimmer but so formidable an accomplishment on its part must be viewed with suspicion. It is unfortunate that Gero (1952) in giving this value does not at the same time reveal the detailed nature of the record taken, the time it was sustained and the other behaviour of the fish concerned. With the body temperature say 10° C. above the tropical sea a burst output of 32×10^5 is not impossible. With part laminar and part turbulent flow this might give a speed of 6 or 7 L for a fish of this size.

(d) *Graphical representation*

Each result in Tables 2 and 3 has to be calculated individually, the speed being based ultimately on the measured weight of muscle in the particular specimen concerned. With two further simple assumptions equations (9) and (10) can be transformed into a relationship between velocity and length which will permit a simple graphical representation of the data.

The weight of muscle (W_m) is undoubtedly related to length, as is the total weight of the fish itself. The weight of all the specimens listed is reasonably expressed by the relationship $W=0{\cdot}01\ L^{2{\cdot}9}$ gm. This is arrived at empirically, is most accurate for the larger forms but is slightly less so for the smaller ones where $0{\cdot}01\ L^{3{\cdot}0}$ would be better. If we assume the proportion of muscle in the body to be constant in specimens of different size (this is not

quite true, Bainbridge (1960)) and fix it arbitrarily at 50 per cent, then we can express muscle in terms of length by :

$$W_m = 0{\cdot}005\ L^{2{\cdot}9} \quad . \quad . \quad . \quad . \quad . \quad (11)$$

Substituting this expression in (9) and (10) and taking the burst power factor of 4×10^5 we thus derive two equations expressing speed in terms of length :

$$V_{\text{Lam}} = 56{\cdot}06\ L^{0{\cdot}56} \quad . \quad . \quad . \quad . \quad (12)$$

$$V_{\text{Turb}} = 62{\cdot}35\ L^{0{\cdot}39} \quad . \quad . \quad . \quad . \quad (13)$$

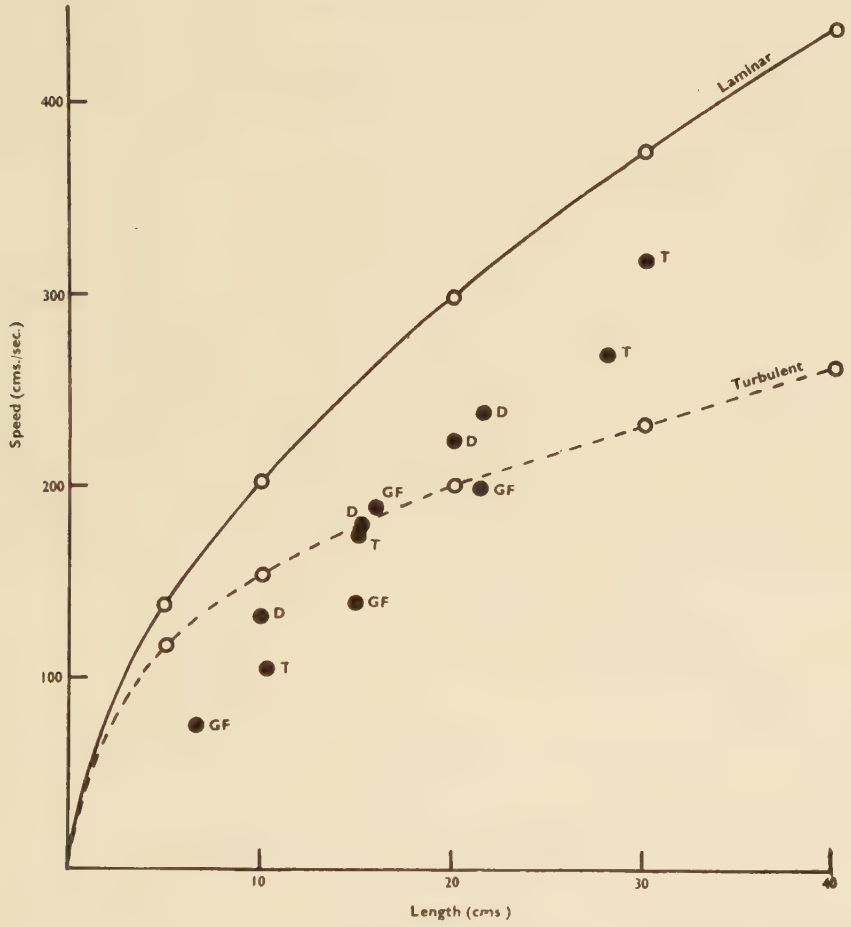

Fig. 1—The calculated relationships between length and speed for a hypothetical fish with completely laminar flow (full line) or completely turbulent flow (dashed line), using a power factor of 4×10^5 ergs/sec./gm. of muscle. For derivation see the text. The points indicate the measured values for a variety of fish : D, dace ; T, trout ; GF, goldfish.

These expressions are plotted graphically in Fig. 1 where the upper, full, line shows the relationship between speed and length for a fish with completely laminar flow and the lower, dashed, line that for a fish with completely turbulent flow. It must be remembered that these are hypothetical fish with 50 per cent of propulsive muscle and weight related to length as $0{\cdot}01\ L^{2{\cdot}9}$.

On this graph are also plotted the maximum speeds recorded for short bursts of swimming by twelve fish from Bainbridge (1960). They comprise four representative specimens each of dace, trout and goldfish and include those listed in Table 2. Figure 1 differs from Table 2 in that the power factor of 4×10^5 is used for the calculated speeds. This has been done because all the measured speeds plotted are of short bursts of swimming. It is again apparent that these recorded results are well within the theoretical maxima with either a fair proportion of turbulent flow or even complete turbulent flow over the surface.

Fig. 2 shows two of these same results—the smallest dace and the largest trout—plotted similarly but on a different scale to allow the inclusion of the measured barracuda, porpoise and dolphin values given in Table 3. In the Table these are all accorded a power factor of 4×10^5 so Fig. 2 and

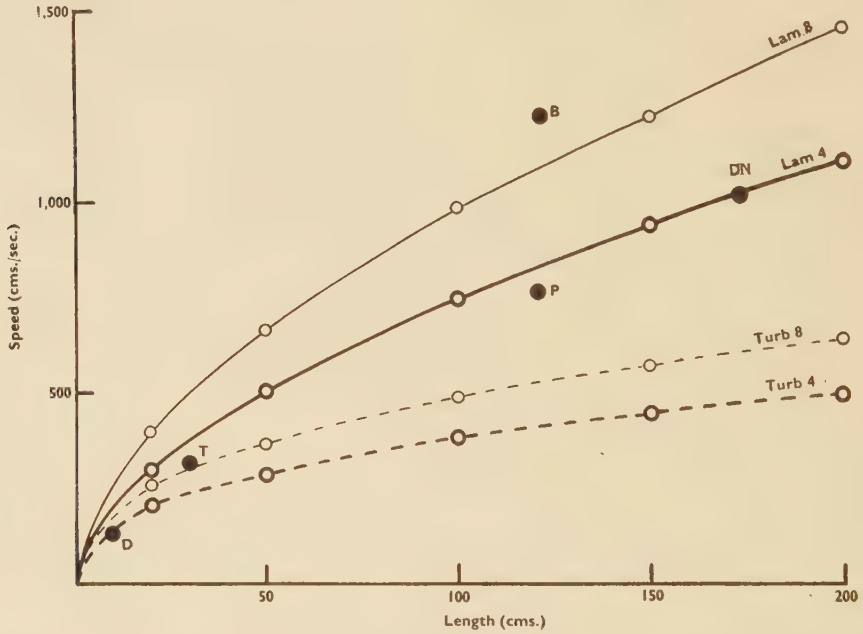

Fig. 2—The relationships shown in Fig. 1 extended to specimens of 200 cms. length. The heavy lines (Lam 4 and Turb 4) are derived using a power factor of 4×10^5 with completely laminar and completely turbulent flow respectively. The finer lines (Lam 8 and Turb 8) are derived using a power factor of 8×10^5 with laminar and turbulent flow similarly. The points indicate measured values for various animals : D, dace ; T, trout ; B, barracuda ; P, porpoise ; DN, dolphin.

Table 3 may be directly compared. The two upper, finer, full and dashed lines further indicate the theoretical speeds expected if a power factor of 8×10^5 is used. The porpoise and dolphin are now brought easily into the partly laminar/partly turbulent region on the graph. This graphical presentation also emphasises how far the barracuda result still appears out of accord with the others.

Fig. 3 shows the data of Fig. 2, with the exclusion of the small dace, on a still smaller scale to allow the inclusion of the measured whale value

given in Table 3 and also a second whale value from Gawn (1948). Both these are fairly near the maximum sustained value with completely turbulent flow. The power factor used to obtain the two lines is 4×10^5.

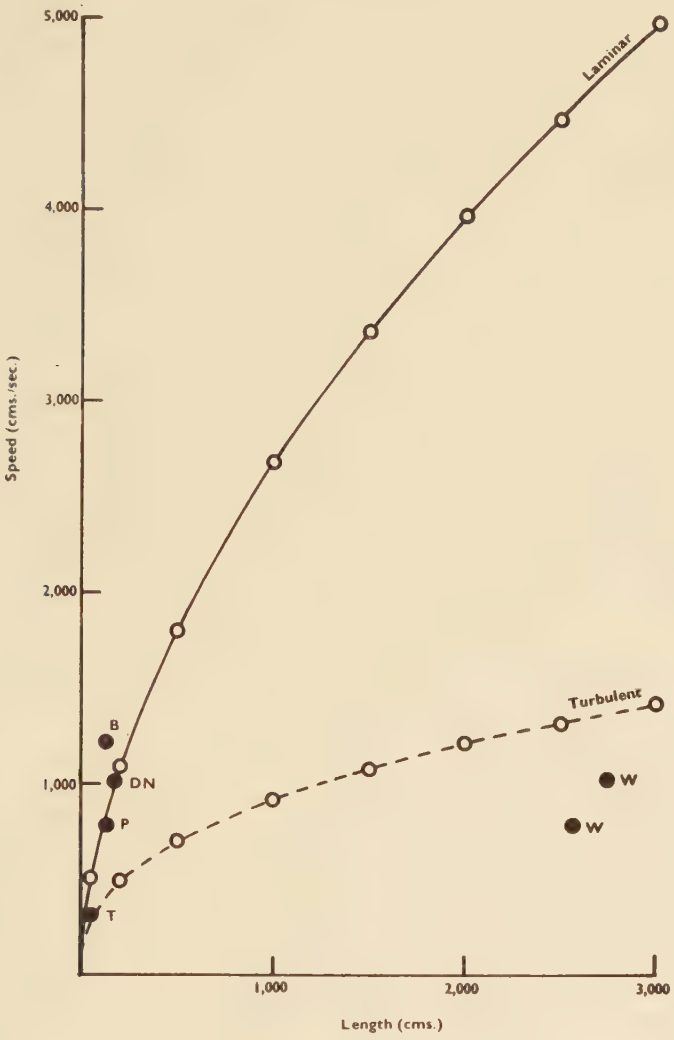

Fig. 3—The relationships in Fig. 1 extended to specimens of 3,000 cm. length, using a power factor of 4×10^5. The points indicate measured values for : T, trout ; B, barracuda ; P, porpoise ; DN, dolphin ; W, whale.

(e) *Conclusions*

Amongst the results presented here the only outstanding problem is thus with fish (or mammals) of an intermediate length, i.e. of the order of 150 cm. The accomplishments of smaller fish can be readily accounted for as can those of the whales. It has already been shown that the speeds attained by these intermediate forms can, certainly in the case of the mammals, largely be

accounted for by variable power factors which may have much higher values than hitherto considered likely. Some surface effect, such as that of Kramer (1960 a & b), may be of consequence and would alleviate the problem to a certain extent. It is still however not possible to account for the record of the barracuda and the possibility of this being a somewhat exaggerated figure must be borne in mind. Really reliable measurements for some of the larger fish and mammals during both bursts of swimming and sustained swimming would still be most desirable.

The differing proportions of muscle in the various specimens listed in Tables 2 and 3 are of course a contributory factor in determining variable swimming abilities and should be considered. The porpoise for example has as little as 13 per cent of its body weight as propulsive muscle while the trout has 63 per cent. These differing proportions have not, however, the marked influence on speed that might at first be expected. With laminar flow they are raised to the power of 2/5 (equation 9) and with turbulent flow to 5/14 (equation 10). This means that doubling the weight of muscle will only raise the speed by a factor of 1·32 with laminar flow or 1·28 with turbulent flow. Nevertheless, this is of some significance and it is of interest that the forms in which the problem is found all have low muscle percentages. All the small fish measured, Bainbridge (1960), showed an increase of 10 to 15 per cent in the relative amount of muscle with increasing length from 5 cm. up to about 17·5 cm. There is just an indication in the trout of something of a decrease with increasing length above this size. Assessment of the proportion of propulsive muscle in a series of fish up to the intermediate size range being considered here would be of great interest. Apart from the particular problem of a discrepancy between the calculated and measured speeds for the fish now being examined one would expect progressively larger forms to need less muscle proportionately to accomplish the same speeds.

Finally, if we attempt to explain the barracuda results by increasing the power factor we create another problem. Unless we suppose barracuda muscle to be endowed with special properties we now find that smaller fish go relatively even more slowly than we might expect them to. That part of their sustained power output determined by circulatory systems and respiratory areas might be affected in two ways by decreasing size. It might either be greater because of the larger proportionate surface area of such smaller forms, or less, because the reduction in sectional area of vessels in the circulatory system must cause increased resistance to the flow of blood. There is immediately however no reason to suppose that these factors should be very different in say a 15 cm. trout and a 150 cm. barracuda. In any case such changes should have little or no influence on power output during short bursts of swimming.

SUMMARY

1. Seven problems still outstanding in the field of fish locomotion are enumerated and briefly considered.

2. One of these, concerning the relationship between power, drag and speed, is examined in greater detail in the light of recent measurements of the speed of smaller fish.

3. Theoretical relationships are developed expressing velocity in terms of length, weight of muscle and a power factor ; and the expected speeds of these smaller fish and some other larger forms are calculated.

4. It is concluded that the measured speeds of smaller fish raise no problems, nor do those of the larger whales.

5. Fish and mammals of an intermediate size do show some discrepancy but it is considered that this could be accounted for by the use of a larger power factor without abnormal hydrodynamic assumptions.

6. Measurements for the barracuda still remain a puzzle and are difficult to account for with even the highest hydrodynamic efficiency.

ACKNOWLEDGMENTS

I am indebted, as ever, to many kind friends for their continuing interest in this work but in this instance particularly to Sir James Gray, F.R.S., and to Dr K. E. Machin.

REFERENCES

Bainbridge, R. (1958 a). The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *J. exp. Biol.* **35** : 109–133.

Bainbridge, R. (1958 b). The locomotion of fish. *New Scient.* **4** : 476–478.

Bainbridge, R. (1960). Speed and stamina in three fish. *J. exp. Biol.* **37** : 129–153.

Bainbridge, R. & Brown, R. H. J. (1958). An apparatus for the study of the locomotion of fish. *J. exp. Biol.* **35** : 134–137.

Breder, C. M. (1924). Respiration as a factor in the locomotion of fishes. *Amer. Nat.* **58** : 145–155.

Breder, C. M. (1926). The locomotion of fishes. *Zoologica, N.Y.* **4** : 159–297.

Brett, J. R. (1956). Some principles in the thermal requirements of fishes. *Quart. Rev. Biol.* **31** : 75–87.

Brett, J. R., Hollands, M. & Alderice, D. F. (1958). The effect of temperature on the cruising speed of young sockeye and coho salmon. *J. Fish. Res. Bd. Can.* **15** : 587–605.

Denil, G. (1937). La mécanique du poisson de rivière. Chapitre X. Les capacités mécaniques de la truite et du saumon. *Ann. Trav. publ. Belg.* **38** : 412–433.

Dickinson, S. (1928). The dynamics of bicycle pedalling. *Proc. roy. Soc.* (B) **103** : 225–233.

Dill, D. B., Edwards, H. T. & Talbott, J. H. (1933). Studies in muscular activity VII. Factors limiting the capacity for work. *J. Physiol.* **77** : 49–62.

Dursy, E. (1863). *Systematischen Anatomie.* 543. Lahr : M. Schauenberg.

Fry, F. E. J. & Hart, J. S. (1948). Cruising speed of goldfish in relation to water temperature. *J. Fish. Res. Bd. Can.* **7** : 169–175.

Gadd, G. E. (1952). Some hydrodynamical aspects of the swimming of snakes and eels. *Phil. Mag.* **43** : 663–670.

Gawn, R. W. L. (1948). Aspects of the locomotion of whales. *Nature, Lond.* **161** : 44–46.

Gero, D. R. (1952). The hydrodynamic aspects of fish propulsion. *Amer. Mus. Novit.* No. 1601 : 1–32.

Gray, J. (1933 a). Studies in animal locomotion. I. The movement of fish with special reference to the eel. *J. exp. Biol.* **10** : 88–104.

Gray, J. (1933 b). Studies in animal locomotion III. The propulsive mechanism of the whiting (*Gadus merlangus*). *J. exp. Biol.* **10** : 391–400.

Gray, J. (1936). Studies in animal locomotion. VI. The propulsive powers of the dolphin. *J. exp. Biol.* **13** : 192–199.

Gray, J. (1957). How fishes swim. *Sci. Amer.* Aug. 1957, 48–54.

Harris, J. E. (1936). The role of the fins in the equilibrium of the swimming fish : 1. Wind tunnel tests on a model of *Mustelus canis* (Mitchill). *J. exp. Biol.* **13** : 476–493.

Harris, J. E. (1937). The role of the fins in the equilibrium of the swimming fish: 2. The role of the pelvic fins. *J. exp. Biol.* **15** : 32–47.

Harris, J. E. (1953). Fin patterns and mode of life in fishes. *In Essays in marine biology.* 17–28. Edinburgh : Oliver and Boyd.

Henderson, Y. & Haggard, H. W. (1925). The maximum of human power and its fuel. *Amer. J. Physiol.* **72** : 264–282.

Hill, A. V. (1939). The heat of shortening and the dynamic constants of muscle. *Proc. roy. Soc.* (B) **126** : 136–195.

Hill, A. V. (1950). The dimensions of animals and their muscular dynamics. *Sci. Progr.* **38** : 209–230.

Hoerner, S. F. (1958). *Fluid-dynamic drag.* Chaps. 13. Published by the author.

Houssay, F. (1912). *Forme, puissance et stabilité des poissons.* 372. Paris : A. Hermann.

Hughes, G. M. & Shelton, G. (1958). The mechanism of gill ventilation in three fresh water teleosts. *J. exp. Biol.* **35** : 807–823.

Kempf, G. & Neu, W. (1932). Schleppversuche mit Hechten zur Messung des Wasserwiderstandes. *Z. wiss. Zool.* **17** : 353–364.

Kramer, M. O. (1960 a). Boundary layer stabilisation by distributed damping. *J. Amer. Soc. nav. Engrs* **72** : 25–33.

Kramer, M. O. (1960 b). The dolphin's secret. *New Scient.* **7** : 1118–1120.

Latimer, H. B. (1944). The prenatal growth of the cat. *Growth* **8** : 205–219.

Lighthill, M. J. (1960). Note on the swimming of slender fish. *J. Fluid Mech.* **9** : 305–317.

Machin, K. E. & Pringle, J. W. S. (1959). The physiology of insect fibrillar muscle II. Mechanical properties of a beetle flight muscle. *Proc. roy. Soc.* (B) **151** : 204–255.

Magnan, A. (1930). Les caractéristiques géométriques et physiques des poissons. *Ann. Sci. nat.* Zool. (10) **13** : 355–489.

Magnan, A. & Sainte-Lague, A. (1929). Essai de théorie du poisson. *Bull. tech. Serv. Aérotech., Paris* **58** : 1–180.

Magnan, A. & Sainte-Lague, A. (1930). Resistance à l'avancement et puissance des poissons. *Bull. tech. Serv. Aérotech., Paris* **71** : 1–107

Nursall, J. R. (1958). The caudal fin as a hydrofoil. *Evolution* **12** : 116–120.

Oosten, J. van (1957). The skin and scales. in *The physiology of fishes.* 207–244. New York : Academic Press.

Parry, D. A. (1949). The swimming of whales and a discussion of Gray's paradox. *J. exp. Biol.* **26** : 24–34.

Richardson, E. G. (1936). The physical aspects of fish locomotion. *J. exp. Biol.* **13** : 63–74.

Rosen, M. W. (1959). Water flow about a swimming fish. *U.S. Nav. Ordn. Test Stn.* T.P. **2298** : 1–96 (Abstract only seen).

Rouse, H. (1946). *Elementary mechanics of fluids.* 376. New York : John Wiley.

Taylor, G. (1952). Analysis of the swimming of long and narrow animals. *Proc. roy. Soc.* (A.) **214** : 158–183.

Taylor, R. J. F. (1957). The work output of sledge dogs. *J. Physiol.* **137** : 210–217.

APPENDIX : DERIVATION OF A POWER FACTOR FROM FROG SARTORIOUS MUSCLE MEASUREMENTS

Hill (1939), in considering the heat of shortening and dynamic constants of muscle, reaches the conclusion that :

$$(P+a)v=b(P_0-P)$$

Where P is the load lifted, a is a force corresponding to the shortening heat of the muscle, v is the velocity of shortening, b is a constant of the dimensions of velocity and P_0 is the isometric tension of the muscle. Rearrangement of this gives :

$$v = \frac{b(P_0 - P)}{(P + a)}$$

Power being equal to Pv ; we thus obtain :

$$\text{Power} = Pv = \frac{Pb(P_0 - P)}{(P + a)}$$

$$= Pb\left(\frac{P_0 + a}{P + a} - 1\right) \quad . \quad . \quad . \quad (1)$$

Hill further gives the experimental relationship :

$$a = 0{\cdot}25\ P_0$$

and shows, by differentiating (1), that maximum power is obtained from the muscle when $P = 0{\cdot}3\ P_0$. Substituting in (1) and rearranging we thus get :

$$Pv = 0{\cdot}38\ b\ P_0$$

The figures for his frog sartorius studies, Hill (1939), p. 174, include the following values :

$$b = 0{\cdot}33/\text{sec. and } P_0 = 1{,}600 \text{ gm. wt./cm}^2$$

Substitution for 0° C. therefore gives :

$$Pv = 0{\cdot}38 \times 0{\cdot}33 \times 1{,}600 \times 981 \text{ ergs/sec/cc of muscle}$$
$$\doteqdot 1{\cdot}95 \times 10^5 \text{ ergs/sec/gm of muscle.}$$

Similar substitutions for 10, 30, and 40° C., using the temperature coefficients given by Hill, provide the figures listed in Table 1.

GENERAL DISCUSSION

Chairman : Professor J. E. Harris, F.R.S.

Prof. Gray : Dr Bainbridge seemed to imply that the swimming of the dolphin raised no hydrodynamic problem. If the dolphin travelling at that speed can maintain laminar flow over its surface, does not this in itself present a problem ?

Dr Bainbridge : The problem can most readily be solved by assuming an increase of the power factor sufficient to allow the flow to be turbulent. This assumption is not inconsistent with our evidence for great variability in the power factor of other animals.

Dr Cain (Oxford) : Could Dr Bainbridge comment on the work of Kramer, suggesting a muscular control of turbulence in the skin of the dolphin, and is there any possibility of a similar method in the case of the teleost fish.

Dr Bainbridge : In Kramer's note in the *New Scientist* he refers to a sort of arch formation in the outer part of the dolphin epidermis. His hydrodynamic models of this consist of a thin rubber lamina supported by a series of small rubber columns enclosing a liquid whose viscosity can be experimentally varied. The combined effect of this flexible rubber layer and of the underlying viscous liquid is to damp out possible turbulence and so to reduce the drag to a value which is about half way between that for completely laminar and completely turbulent flow. The experimental effect in the models is clear, and the correspondence with the structure of the dolphin skin appears to be quite close. I think it unlikely that this could happen in bony fish.

Dr Marshall (British Museum) : The same cellular structure occurs in the skin of the marlin where it is filled with oil. In the tunny sheets of fat separated by connective tissue may serve a similar purpose, and one should not therefore rule out the possibility for bony fish. In marlins of course most of the scales are embedded and the spongy surface is completely in contact with the water.

Dr Murray (Birmingham) : Dr Bainbridge has suggested that turbulent flow is a bad thing and laminar flow is good. Mr Watts says turbulent flow is good. What is the answer to this ?

Mr Watts : In our own " turbulent " ship designs the Admiralty coefficient is 0·30 lb. of oil per hour per horse power or better ; the Admiralty considers a figure of 0·33 for the normal type of design is good going.

Dr Bainbridge : There is a clear and measurable difference of 10-fold between the drag of a surface over which the flow is laminar as compared with one over which it is turbulent. These are laboratory studies on submerged surfaces ; the behaviour of Mr Watts' ships represents a different approach ; the deduction from the better performance of these ships appears to be that some factor in the flow allows them to move more efficiently.

Prof. Gray : I think another factor comes in. When you turn a stream of water onto a body with sufficient speed to create turbulent flow, there comes a time when the flow breaks away from the surface and forms two great lines with a mass of dead water in behind the body. If, however, you make the inflow turbulent, the breakaway point is delayed so that there is less of this disturbed mass which so greatly increases the drag. Under certain circumstances therefore you can reduce the drag by this means.

Dr Bainbridge : A third phenomenon known as separation is obtained for example in high speed aircraft ; whether it could contribute materially in the case of a fish is not known but it may in the ship. In either case, the extreme limits are those of completely laminar and completely turbulent flow; the drag will never be more than that determined by the turbulent drag coefficient.

A NOTE ON THE SHAPE OF FISH MYOTOMES

BY

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The peculiar shape of the muscle blocks which make up the lateral body musculature of fishes has always been of interest to zoologists. The most recent work on this subject is that of Nursall (1956), who gives an adequate bibliography of earlier studies. It is the purpose of the present note to point out a feature of myocommata and intermuscular bones which has hitherto been ignored. The relatively inelastic myocommata and intermuscular bones can prevent adjacent muscle blocks from working properly. This interference can however be reduced to a minimum if the bones or septa lie at the correct angle to the muscle fibres.

It is clear that an intermuscular bone lying parallel or nearly parallel to the vertebral column of a fish will prevent the contraction of muscle fibres lying in its vicinity, and such muscle fibres would then be completely ineffective for locomotion. It is equally true, though less immediately evident, that intermuscular bones which lie in any direction in a plane at right angles to the vertebral column would be an impediment. Muscles, when they contract, must increase in cross section, and this increase would necessarily put any bone lying in the transverse plane in tension, once again impeding the successful contraction of adjacent fibres.

In any block of muscular tissue which is contracting in one direction, there must exist some line, at an angle to this direction of contraction, which will neither extend nor shorten when the muscle block contracts. A bone lying in this position will exert no restriction on the muscle field in its vicinity. It can readily be calculated that this direction lies at an angle of arctan $\sqrt{2}$ or 55° to the direction of the muscle fibres. Unfortunately the author found only one animal which agreed with this theory (*Ichthyostega*), and this is extinct !

The question of myosepta is less easy. It is impossible to find a completely strain-free surface, and there are not enough data to indicate what would be the nearest approximation to such. We might however guess that the best position for a myoseptum would be that in which neither its thickness nor its surface area changed as a result of muscular contraction in the neighbourhood. If the surface of any small element of the myoseptum is considered as a plane, its thickness at that point must lie in the direction previously calculated to give no change in length ; the plane at right angles to this direction will then necessarily be unchanged in area. It follows that any line lying in this myoseptal plane must be at an angle of arcot $\sqrt{2}$ or 35° to the muscle fibres ; a pencil of such lines through any one point will lie on the surface of a cone whose axis is parallel to the muscle fibre direction and whose semi-vertical angle is 35°. A single myoseptum need not however lie entirely on such a

simple conical surface ; the direction of the cone can change at any point from an anteriad facing one to a posteriad facing one so that a W-form is as effective as a V-form for the section of the myoseptum. Such a system of cones reflected (in the optical sense) in a vertical transverse plane is a characteristic feature of myoseptal arrangement.

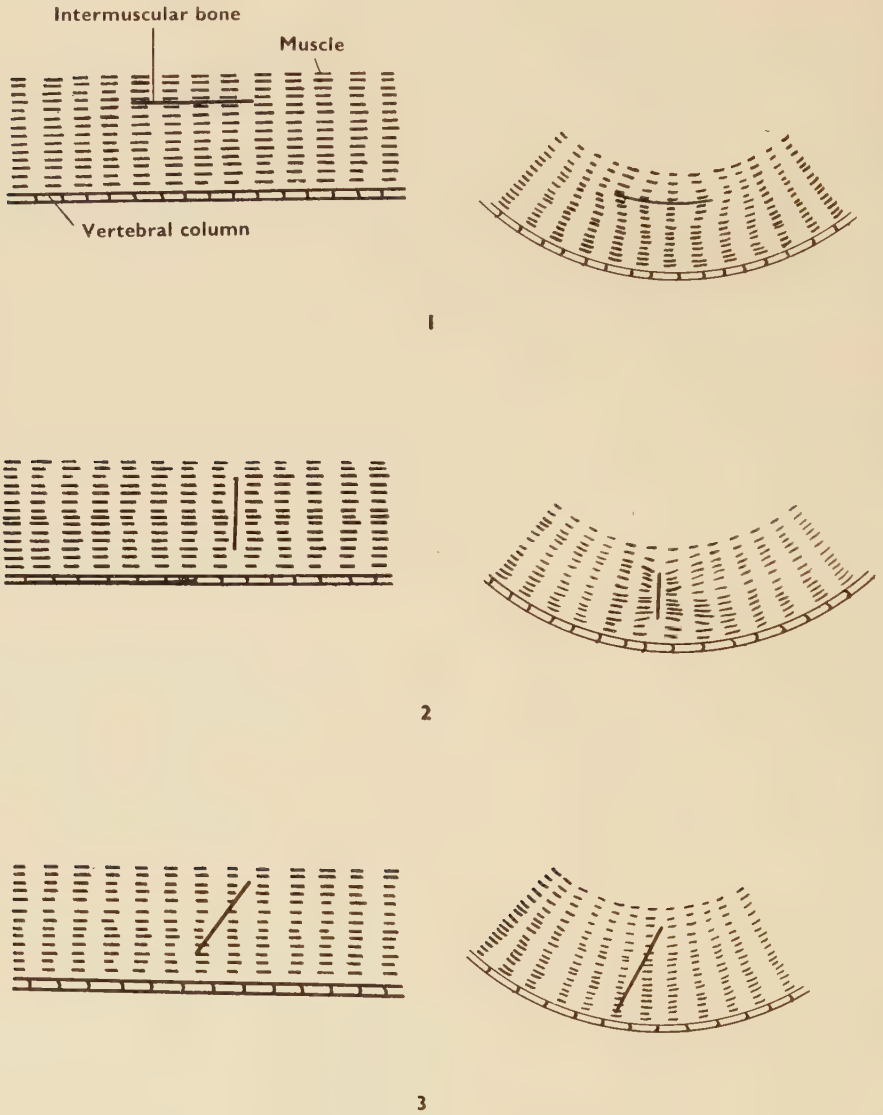

Fig. 1—The effect of an intermuscular bone on the contraction of a block of muscle fibres. The bone is shown (1) parallel (2) at right angles (3) at 55° to the direction of the fibres.

Once again it is unfortunate to have to admit that experimental comparison of this theory with the morphological facts is acceptable only in those animals where the cone angle shows a good deal of variation within one individual.

In fixed specimens of the dogfish (*Scylliorhinus canicula*) the semi-vertical angles vary from 25° in the tail region to 55° in the trunk, so that almost any theory would fit the facts. At the same time, it is clear that the basic assumption underlying the present theory—that we are dealing with a uniform mass of contractile tissue in which the direction of contraction is always parallel to the longitudinal axis of the body—is an oversimplification. In the absence of a more satisfactory explanation of the shape of the myoseptum, the idea may at least be worth further examination.

Finally, though this idea may shed some light on some of the problems in this subject, it certainly does not solve them all. It suggests where bones and septa ought to be to create the minimum embarrassment, but it does not show why they are there in the first place. They can hardly have persisted for three hundred million years as a useless ornament.

REFERENCE

NURSALL, J. R. (1956). The lateral musculature and the swimming of fish. *Proc. zool. Soc. Lond.* **126** : 127.

THE RELATIONSHIP OF FISH LOCOMOTION TO THE DESIGN OF SHIPS

BY

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CONTENTS

	Page
Introduction	37
Early attempts in relationship	37
Swim bladders into deck tanks	38
Fins and turning circles	39
Gills, bow waves and turbulence	40
Fish shapes and hull forms	41

INTRODUCTION

The preparation of this paper was the first attempt at a rationalization of ideas and experiments which have been evolved during a lifelong interest in ships and fish. Nine years in the Royal Navy followed by forty years in shipping and rather more than the combined total of fifty years a fisherman has offered plenty of scope and has been a happy illustration of the adage " Learning can be fun ". But it hardly seems sufficient qualification to take part in a symposium on aquatic locomotion, especially as I freely admit that its relation to ship design has been almost entirely by guesswork. However, since I am grateful for the help and advice which I have received from my scientific friends I hope that some of the following applications and adaptations from fish to ships may be of interest.

EARLY ATTEMPTS IN RELATIONSHIP

It was as long ago as 1927 when it first occurred to me that there were various ways in which the design of ships might be adapted more closely to those fish which during the course of evolution had become the strongest and fastest in the sea. At this time there was an enquiry for three new ships to ply in the coal trade between Sydney, Cape Breton and St. Lawrence ports. Up to that date single deck ships for this business had always been constructed with stanchions in the holds to stiffen the decks. These obstructions caused much expense to charterers because trimmers had to be employed to move the coal from places the grabs could not reach and the crane drivers did much damage when swinging their grabs to get as near to the corners as possible.

Nature provided the answer. The main strength of a fast-swimming fish is the backbone and the muscles around it whilst the belly muscles are comparatively weak. So s.s. " Watford " and her sisters were built with two continuous deck girders carrying the heaviest plating in the ship, the strength gradually diminishing the deeper the draft. In other words, these three ships were designed in suspension instead of from the bottom up.

The main object of large open holds for carrying bulk cargoes was achieved and in addition much greater deck strength against bad weather.

It was in these ships also that the first tentative steps were taken towards the modification of the hull form away from the orthodox streamlining towards the deliberate creation of turbulence along the ship's side which not only reduced skin friction but led eventually to the unorthodox bow and stern forms which have improved the performance of our later designs.

During the 'thirties when three different classes of ship were designed and built these ideas were further developed ; but it became obvious that until something was done to reduce pitching much of the increased efficiency was being lost in bad weather. A partial solution was found in greater buoyancy forward and aft, but the disadvantage of this was that in heavy weather the fuller lines held the ship back. The solution adopted in 1938 for the last class was a break in the section of the bow and stern forming knuckles. These knuckles maintain buoyancy above while permitting a fine entry forward and a fine run aft. They help to lift a heavily laden ship above either head or following seas so that she slides over the water rather than pounding and pushing her way through it with the seas piling inboard.

It is not of course suggested that these knuckles were in any direct sense derived from fish forms, but they are nevertheless an attempt to give ships a balanced movement in the water, the element which, like fish, they must be designed to use efficiently as their medium of locomotion.

SWIM BLADDERS INTO DECK TANKS

Immediately after the war, plans were made for the building of three general cargo liners for the North Atlantic. In contrast to bulk carriers these ships have a high cubic capacity and present many different problems of stowage and stability. This is due to the varying weights and character of the consignments loaded and discharged on any one voyage. The distance between the centre of gravity and the metercentre in a ship is all important. Should they coincide the vessel would turn turtle, but the greater the distance the greater the roll. So the aim must be to reduce the margin within the limits of safety by the stowage of cargo in strategic positions according to bulk and weight. The main difficulty in achieving the cargo stowage plan that would theoretically be the most efficient is that the various consignments never come forward or have to be discharged in the required order. Therefore it was found that in certain conditions in the North Atlantic these three ships, like others in the same trade, rolled excessively (i.e. up to forty degrees in twelve seconds). Rolling in a ship destroys the lines, wastes effort and creates inefficiency ; it is obvious that the effect on fish would be similar, which is presumably why they are equipped with swim bladders to maintain their equilibrium. These natural stabilizers seemed to offer the possibility of a further useful adaptation.

In 1949 the first of the " Windsor " class was being designed and into them were incorporated deck tanks or nautical versions of the swim bladder. Four of these tanks, capable of holding between one and two hundred tons of water ballast, were built into the strength deck in the hope that they would provide a

balancing factor to counteract awkward distribution of cargo. Experience has shown that used judiciously these can reduce rolling from forty degrees to ten degrees in twelve seconds and not, as with mechanical stabilizers by wracking the hull through trying to wrench it against the force of the waves, but persistently and gently to right the ship as the swim bladder does the fish.

FINS AND TURNING CIRCLES

It was Sir James Gray, to whom I am most grateful, who suggested that I might try to find out how the blue tunny catches the horse mackerel, as in theory both are capable of the same speed.

The only difference I could see in the Museum specimens was that the blue tunny has small lateral fins forward of the tail and the mackerel none.

As the tank model of the " Windsor " class was still intact at the National Physical Laboratory it was comparatively easy to design and fit fins that were roughly proportionate to those of the blue tunny. But on being tested in the tank no change in the performance of the model was discernable. This, however, did not deter me from having fins fitted to the third ship of the class, m.v. " Woolwich ", which had not left the builders' yard. I felt there was a good chance that on full scale they would show some effect at sea. And indeed they did ; although it was not any considerable increase in speed. Unexpectedly, though, not altogether surprisingly the turning circle of m.v. " Woolwich " was reduced to almost half that of her sister ships. She needed less helm and made far less drag.

Tables are available showing a comparison between m.v. " Woolwich " and " Wokingham ", showing a turning circle of about 800 feet in under seven minutes for the former compared with about 1515 feet in seven and a half minutes by the latter without fins.

Due maybe to the need for less helm and the reduction in the drag we are also inclined to give the fins credit for both a small increase in speed and a slight reduction in bunker comsumption.

Similar fins with appropriate modifications according to the different hull forms have since been fitted to the other seven ships in our fleet, making them all easier to handle, especially in pilotage waters.

In our latest design, the first of which, m.v. " Willesden ", is now under construction, the lines and the fins are inspired by those of the mako shark.

When I visited The Marine Laboratory at the University of Miami, I was told that the remains of swordfish had twice been found in the stomach of a mako. The swordfish was thought to be the fastest fish in the sea, but the mako apparently eats him. In view of this it was interesting to find on examining the casts that the lateral fins in front of the tail of the mako shark are differently shaped and larger in proportion to the body than those of the tunnies.

Therefore, although m.v. " Willesden " is twenty-five feet shorter than her two predecessors, her fins are roughly three feet longer and two inches wider than any fitted previously. The peculiar shape of the mako's fins have been followed. The effect of these changes will not be known until the ship goes through her trials and sets off on her maiden voyage in the spring.

GILLS, BOW WAVES AND TURBULENCE

I have already made a brief reference to the deliberate creation of turbulence along our ships' sides and should now like to explain some of the reasons for this rather eccentric departure from the classic perfection of streamlining.

Examination of fast-swimming fish in prime condition shows that the shoulders are prominent and covered by fat and muscle over which the water is exhausted from the gills. The oxygen and certain minerals abstracted from the water by the gills means that a different liquid is being ejected from what is surrounding the fish ; and suggests the destruction of stream-lines. The tunnies, in particular, have strong corselets of much heavier build than the rest of the body coverings ; indeed in some cases the corselets are the only scales.

Some years ago I was fortunate enough, when in a ship lying off Barbados discharging cargo at night, to see eight tuna packed like a rugger scrum, cutting swathes through the fry which had been attracted by the ship's lights. the three leaders hurtled their way through the little fish. The space between them, aided by their gill discharge and shoulder wash, seemed to become a funnel to concentrate the feed to the second row and from their shoulders in turn what was left was projected into the mouths of the back row. This went on for some time round and round the ship in the full glare of the cargo clusters making a zigzag silver stream of the fry as the pack passed through them. Behind the shoulders of these fast-swimming fish it was obvious that the water was turbulent without any detrimental effect on their speed.

It had for some time been apparent that the thickening of the hull forms at the shoulders in our earlier ships had not been disadvantageous and this experience strengthened my growing conviction that there might be actual benefits to be gained from turbulence.

There is one advantage shared by Jonah and the ship designer who went to sea—they both had the sea outside them and could " listen in ".

For this purpose I use a stethoscope inside the ship's hull and it is possible from the forepeak to the stern gland to listen to the different waters sweeping by and chalk in the different flows.

With a fine entry the ship cleaves the water quietly ; then at the shoulder the sound deepens as it throws off the weight of water in a bow wave which leaves the side at an angle of between nineteen and twenty-three degrees according to the draft and trim. Behind this wave the sound changes to the swishing noise of converging vortices of frothy, turbulent water. This turbulent noise persists along the flat sides of the hull, until at the beginning of the run aft to the propeller there is another change. It is at this point that solid water begins to surge upwards from underneath the flat bottom of the ship on to the propeller. It seems that the lateral fins along the run aft have the effect of directing this surge on to the lower half of the propeller, while the lighter turbulent water is thrown on to the top half, giving something of the effect of a fly-wheel.

You may think that I have not succeeded in demonstrating any very close connection between gills, bow waves and turbulence and I can only reply that these are some of the ingredients of successful ship designs, taken from

m.v. "WOOLWICH"—7,668 gross tons, fitted with lateral fins and with nine deck tanks built into the strength deck.

Note:- The ridge of solid water off the "shoulders" and lack of other hull produced waves.

m.v. "WEYBRIDGE"—Cargo liner of 9,221 gross tons fitted with lateral fins and with two deck tanks.

Note:- In addition to m.v. *Woolwich* "shoulders" of heavier design this later class ship produces greatly increased turbulence along ship's side, thus reducing skin friction with increased speed for lower power.

what no doubt may seem to marine biologists rather peculiar ideas about the shape of fish and how they swim.

FISH SHAPES AND HULL FORMS

By this time I was satisfied that these somewhat rough and ready adaptations from fish to ships had proved their usefulness, and it seemed probable that more exact information might yield further possibilities. I was greatly assisted by Mr N. B. Marshall and Dr E. Trewavas of the British Museum of Natural History, who gave drawings and information to me and allowed me to handle specimens. But somehow dead fish were much less inspiring than live ones from my point of view. In particular, I began to wonder how closely the hull forms of our ships now approximated to those of live fish. To my long interest in salmon from a fisherman's angle was added a curiosity concerning the shape of their bodies and their extraordinary powers of locomotion.

On the Creed the fish demonstrate these powers by getting up 200 yards of continuous falls which rise 100 feet. Their first resting place, the Peat stack pool, is a mile and half from the sea and 150 feet above sea level.

It was easy to examine freshly killed salmon on the river but to get accurate measurements and comparisons I should like to have had live fish in my drawing office. I asked Mr Marshall whether it would be possible to make casts on the spot of live fish and he suggested asking for the collaboration of Mr Stammwitz. Together they worked out a method whereby the fish were taken from the water and placed while still alive into moulding boxes filled with a nearly similar solution to which a solidifying agent was then added. Whilst it was setting the fish were held still and upright by their tail and dorsal fins so that the resulting models gave an almost exact outline of their swimming shapes. Casts were made by this method of fresh run fish and others which had been up for some weeks and were near to spawning.

All exhibited a somewhat unorthodox shape by taxidermy standards : a dead flat belly and as flat as no difference at the throat and abaft the anal fin. The stale fish had altered surprisingly little since leaving the sea in spite of being in three cases within a few days of spawning. On dissection it was found that the ova, instead of distending the outline as in animals, were held high up under the backbone. Indeed, the organ most affected by the growing ova was the swim bladder which was very restricted. Perhaps this accounts for the sluggishness of " back end " fish.

PELVIC GIRDLE IN AMPHIBIAN LOCOMOTION

BY

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CONTENTS

	Page
Introduction	43
Previous work	43
Structure :	
1. Pelvic and sacral organization of *Xenopus laevis*	45
2. Pelvic and sacral organization of *Rana temporaria*	48
3. Pelvic and sacral organization of *Discoglossus pictus*	51
Conclusions	53
Acknowledgments	54
Addendum	54
References	56
General discussion	57

In Amphibia, the junction between the pelvic girdle and the backbone, at the pair of ilio-sacral articulations, has frequently been described as if it were a symphysial joint where very little movement would take place. This assumption has been made in anatomical and in locomotor studies.

There is in fact a considerable movement here, at least in *Salientia*. In *Rana*, the ilia may rotate through an angle of over 90° on the sacral ribs, in the vertical plane. This vertical bending and unbending is used during a strong leap.

In the primitive toad-like *Discoglossus* the sacrum can be slewed laterally on the pelvis through 20° to either side. The movement is used in turning, both to take food and in locomotion.

In the aquatic batrachian *Xenopus*, the sacrum can slide backwards and forwards on the pelvis, producing a considerable shortening and lengthening of the whole animal. This movement is probably used in driving into sub-aquatic mud.

INTRODUCTION

I shall attempt here to describe, in the Amphibia, the junction between the hindlimb-girdle and the backbone, and to show that, at least in the anuran Amphibia, this iliosacral joint is movable and has some importance in their locomotion.

In Anura the pelvic girdle has been regarded, by some experienced workers, as rigidly attached to the sacral vertebra, but others have considered the articulation to be flexible. This disagreement, although it has continued over many years, could not be called a controversy for little emphasis has been given to the matter.

PREVIOUS WORK

It is not easy to give a brief summary, because comments on the mobility or the rigidity of the ilio-sacral articulation of the Anura have usually been

made *en passant*, during discussion of other subjects. The writer's opinion is often only implied. Ridewood (1897) stated that the ilia are free to slide backwards and forwards on the sacrum, especially where the sacral diapophyses are expanded in the horizontal plane. Boulenger (1896), mentioning *Discoglossus*, and Nauck (1938), mentioning *Pipa* and *Xenopus*, also considered there was a sliding action, at least when the sacrum is expanded. Nauck quoted some nineteenth century work in support of his statement.

On the other hand, Gadow (1901) considered the " Ilia . . . firmly attached to the sacrum " in frogs. Green (1931) held that expanded sacral diapophyses produced a " greater rigidity ", and Parker (1932) that they gave a " larger surface for rigid attachment of the ilia ". Noble (1931), who will be quoted later, and Gregory (1935) appear to me to have implied that there is no movement. Mookerjee (1931) wrote " In each of the four cases, viz. *Rana*, *Bufo*, *Bombinator* and *Xenopus*, the transverse processes of the ninth vertebra articulate on the side of the ilium a little below its tip—contrary to the views of Balfour, Marshall, and Gadow ", i.e. the ninth vertebra articulates at a *constant* position with the pair of ilia in these animals. The only movement then possible would be a vertical rotation of the sacrum (and, with it, the trunk and head) about the two ilial articulating surfaces : this movement could only occur in *Rana*, of these four, which has narrow ilio-sacral articulations, about which considerable rotation is possible. Saunders & Manton (1959) stated that in *Rana temporaria* " The pelvic girdle is fixed to the sacral vertebra and there are no muscles to move it relative to the body ".

Where the articulation was considered to be a fixed one, no doubt the coccygeo-iliac muscles were supposed to act on the urostyle, and the ilio-sacral muscles to act on the diapophyses of vertebrae in front of the sacrum. Grobelaar (1924) worked extensively on *Xenopus*. He believed the ilia of *Xenopus* to be rigidly attached to the sacrum. Since the urostyle is fixed to the sacrum in *Xenopus*, it is surprising that Grobelaar did not notice that the coccygeo-iliac muscles, which he described, had in his view no apparent function.

Barclay (1946) took ciné X-ray photographs of the toad *Bufo* during walking movement. He does not appear to consider that there was movement in any part of the backbone or at the ilio-sacral angle but in fact there may have been no movement here during walking.

Howell (1944) wrote that " the leaping ability of frogs is due . . . in minor part to refinement of body form, such as shortening of the trunk and character of lumbosacral joint ". He does not expand this remark, going on to say that the saltatorial specializations are related rather to the forelimb than the hindlimb. While the movements of the scapula are considered in relation to the action of the forelimb, even recent workers on the hindlimb of Anura (Ritland, 1955, Dunlap, 1960) have not referred to the possible effect of an ilio-sacral movement on hindlimb action.

It is reasonable to say that the views of Ridewood, Boulenger and Nauck have not yet been widely accepted. Most authors appear to have considered the ilio-sacral articulation to be more or less rigid. Certainly, movement at the ilio-sacral joint has not been considered to be an important factor in anuran locomotion.

STRUCTURE

Turning first to the skeletal apparatus involved, it is important to notice that in anuran tadpoles the vertebrae and the girdle are quite well developed before they become articulated together. There is a stage when each iliac cartilage extends from the pubic symphysis in an antero-dorsal direction to end freely, short of the vertebral column (cf. Boulenger, 1896, Fig. 39). During individual development the ilio-sacral articulation must therefore tend to be flexible when first effective. Considerable parallel evolution must be expected between species where the metamorphosing tadpole is turning to either climbing, swimming, crawling, or jumping forms of locomotion.

In the adult there is a considerable difference between the ilio-sacral region of the skeleton of frogs and of toads. In a frog, e.g. *Rana temporaria*, the pair of transverse processes or diapophyses of the sacral vertebra project latero-caudally and have a rod-like or subcylindrical form. The pair of ilia project antero-dorsally and they also have a rod-like form. At the left and right sides the two rod-like extremities meet tip to tip at the corresponding sacro-iliac articulations, as illustrated by Marshall (1928) and by Boulenger. In this region the drawing of Marshall is more accurate than that of Boulenger but unfortunately suggests that the ilia end in a position dorsal to the sacral processes.

In other Anura such as the common toad, *Bufo bufo*, the sacral diapophyses are distally expanded in the horizontal plane so that from above or below they have the outline of a pair of wings. Each ilium meets the sacral process along the under-side of the broad distal edge of the wing so that the articulation here extends some distance, in a direction parallel to the long axis of the body (cf. Boulenger, Fig. 81). Noble (1931) wrote : " The pelvis of *Salientia* is especially characterized by its long ilia which make a ligamentous connection with the diapophyses of the sacral vertebrae. There may be two or three of these pairs of diapophyses but one is the rule. In some Salientia these diapophyses may be greatly expanded. The functional significance of this modification is, however, not clear ". This is the apparatus whose function I shall try to elucidate.

1. *Pelvis and sacral organization of* Xenopus laevis

I became interested in the problem of the ilio-sacral articulation in the case of *Xenopus*, so the account begins with this animal. A third-year student was comparing the anatomy and function of the musculature of a South African Clawed Toad, *X. laevis*, with that of *R. temporaria* and noticed that there was considerable fore-and-aft movement between the pelvic girdle and the backbone. This observation was followed by more extensive work during that year, and the conclusions were briefly published recently (Palmer, 1960).

In the words used in her own short account : " Dissection of a freshly killed *Xenopus* shows that the vertebral column slides freely backwards and forwards on the pelvic girdle, in a groove in the medio-dorsal aspect of the ilia. In the living animal a slow-motion cinematograph film revealed a 20 per cent range of extension and contraction of the total body-length as a result of this movement ; in one specimen the " normal " trunk-length of 9·5 cm.

could be contracted to 8·5 cm. or, when the hind-feet pushed against a solid surface, expanded to 10·0 cm." In her paper she illustrates the skeletal apparatus and the muscles which effect the movement.

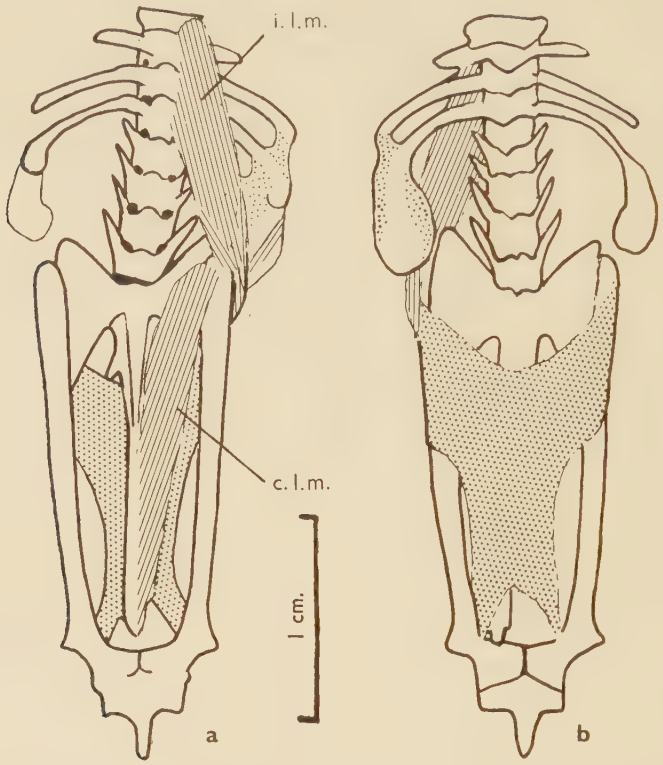


Fig. 1—Vertebral column, urostyle and pelvic girdle of *Xenopus laevis*, with retracting and protracting muscles on one side ; drawn from photographs of dissections. (a) ventral aspect. (b) dorsal aspect.
c.i.m. coccygeo-iliac muscle. ; *i.l.m.* ilio-lumbar muscle. ; Mechanical *stipple* lumbo-dorsal fascial band.

I have made dissections to show this structure. In ventral aspect (Fig. 1 a) can be seen the wing-like sacral vertebra with part of its distal edge just clear of the iliac groove in which it slides. The ribs ankylosed onto the second to fourth vertebrae can be seen, and also the fusion of the urostyle with the ninth (sacral) vertebra. On the right of the figure, the muscles which link the vertebral and pelvic parts of the skeleton have been left in position :—*M. coccygeoiliacus* which projects the vertebral column forwards and *M. iliolumbaris* which retracts the vertebral column. This second muscle is inserted on the ventral aspect of the first to fifth vertebrae, except for a small slip running to the cartilaginous tip of the last rib. Excitation of these muscles elicits a fore-and-aft movement of the vertebral column ; unilateral excitation produces the same effect, causing only a slight lateral movement. Yet the head can be swung strongly to the side, for the various intervertebral muscles are well developed and the vertebrae are strongly opisthocoelous in plan view. Each

vertebra can therefore rotate laterally through a wide angle on its " next astern ".

The dorsal aspect (Fig. 1 b, and Pl. 1) shows more clearly how it is possible for the two parts of the trunk system to slide on each other. There is a wide fascial band, *F. lumbodorsalis*, much stronger than other fascia of the region, between the two iliac arms of the pelvis. The band passes dorsal to the sacrum and urostyle and to the caudal part of the *M. longissimus dorsi*. The band will provide a smooth surface for this muscle sliding beneath it and will also help to keep pelvis and sacrum closely applied together. The band is attached to the front third of each ilium and to a process on the upper caudal aspect of the ilium. The rest of the body musculature is attached to the pelvic section or to the vertebral section but not to both, and so is not torn when the two mechanical units move towards or away from each other. For example, the attachment to the pelvis includes very large *external iliac muscles* from the femur, which extend onto the fascial band, and large *external oblique muscles* which run laterally from the pelvis. Details of the trunk musculature can be seen in the figures of Keith (1905), Grobelaar (1924) and Millard (1941).

In this species, then, the ilio-sacral articulation is movable, and probably does move during normal locomotion. As Palmer states, " In *Xenopus*, the whole propulsive effort in swimming and in burrowing occurs in one plane. The forward thrust of the hind-limbs must be transmitted through the coccygeo-iliac muscles. These muscles, together with their antagonists, will provide an effective shock-absorbing mechanism and assist in drawing the hind-limbs forward into the mud during under-water burrowing ".

This is probably true of the other pipids (Aglossa) also. X-ray photographs of *Pipa pipa*, the Surinam toad, suggest that the vertebral column is here too shifted backwards and forwards on the pelvis. *Pipa pipa* and *Hymenocheirus boettgeri* also exert " the whole propulsive effort in one plane ". The vertebral, sacral and pelvic skeleton is similar among New and Old World pipids (e.g. they possess three pairs of ribs, opisthocoelous vertebrae, expanded sacral wings with a straight distal edge, and a fixed urostyle). The pipid genera also have similar hind-limb musculature (Dunlap, 1960).

However, one matter remains unsettled. The sliding articulation of the pipid toads may be primarily not locomotor but respiratory and hydrostatic in function, for the following reasons. *Xenopus* and *Pipa* often adopt a bipedal or even vertical stance : they may just touch the water surface with their finger-tips or the bottom with their toes, and may alter their stance without limb movement. Evidently the pressure in the lungs can be precisely adjusted, as in a Cartesian diver, Secondly, these genera may inhale air rapidly and noisily, which must also require good muscular control of lung volume. Beddard (1895) and Green (1931) have described this special ability of pipids. The structural basis has been attributed to three groups of special muscles which pull directly on the lungs. In *Xenopus*, one of these muscles is of special interest because it takes origin from the ilium, the slender *ilio-pulmonary* muscle ; in *Pipa* there is a similar muscle but it takes origin from the femur ! Keith (1905) is the only worker to give clear figures of the whole apparatus ; his important account has been overlooked, except by Nishi (1938).

Now the tadpole of *Xenopus* already possesses an air-space which is hydrostatically important, for it is well known that the tadpole remains poised in midwater for long periods, counter-acting the upward force from the air-space by the movement of its tail. At metamorphosis, an alteration in trunk-length, effected by the newly-forming ilio-sacral articulation, may become an important means of adjusting the air-volume in the lungs. But alterations in trunk-length have not been observed in adults of *Xenopus* when they are stationary and adjust their stance, so that this explanation is unlikely to be correct.

I shall now try to show that ilio-sacral movements occur in other Anura and are there primarily of locomotor function. Such a conclusion would make it more probable that in pipids too the movement had a mainly locomotor function.

2. *Pelvic and sacral organization of* Rana temporaria

Observation of the common frog under natural conditions shows that there is in fact considerable movement at the ilio-sacral articulation, and that this movement is used during locomotion. The action is a hingeing, not a sliding, one, and lies almost entirely in the longitudinal vertical plane.

X-ray photographs of squatting frogs and " standing " frogs (i.e. reaching up, against a vertical wall) show the general result at once (Plate 1, R). The vertebro-iliac and vertebro-urostylar angles were measured (by another Bristol student : Passaway, 1960). The vertebral axis was taken to be a line through the last three vertebrae (these retained the same relation to each other), and the iliac axis to be a line joining the sacral articulation and the acetabulum. Photographs show a vertebro-iliac angle of 147° and 160° for two " standing " frogs, and 90° and 95° for squatting frogs, so that the ilia can rotate on the sacrum through about 60° during this change in posture. The vertebro-urostylar angles for " standing " frogs were 167° and 180°, and 125° and 120° for the squatting position. The urostyle therefore moves through a similar, perhaps slightly smaller, arc.

The mechanism of the movement can now be considered (Fig. 2). The relevant parts of the skeleton of the common frog are very different from those of *Xenopus*. The sacral processes have a subcylindrical form and the ilia do not have a groove on their dorsal surface ; the ilio-sacral articulation is enclosed in a small joint-capsule ; the urostyle has a flexible articulation with the sacral vertebra ; there are no ribs ; the successive transverse processes are of similar length.

The muscles of the region are also different from the corresponding ones in *Xenopus* ; they are generally similar to those of *R. esculenta*, as described by Haslam (1889). The *M. coccygeo-iliacus* is altogether broader and shorter than in *Xenopus*, and its fibres run in a more transverse direction, at about 45° to the long axis of the urostyle. *M. ilio-lumbaris*, taking origin from the end of the ilium, now runs anteriorly to end on the distal parts of successive transverse processes. It retains segmental organization to some extent.

In dorsal view, the coccygeo-iliac muscle can be seen to have a more extensive origin and insertion than on the ventral side. This applies also to the ilio-lumbar muscle, which is more developed on the dorsal aspect of the

transverse processes. Its attachment to the ilium is by two heads, in *R. temporaria*, as Passaway has observed : one is medial and the other lateral to the joint-capsule, but both are on the dorsal side of the joint. The ilio-lumbar muscle therefore produces its effect on the dorsal side of the vertebral axis, unlike the condition in *Xenopus*.

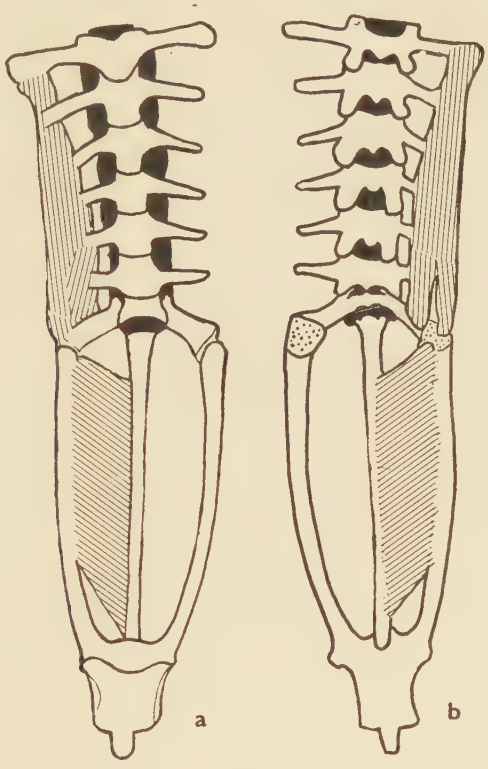


Fig. 2—Drawing, as Fig. 1, of *Rana temporaria*. The atlas and axis are not shown.

It is not easy to separate the ilio-lumbar muscle from fibres medial to it, belonging to *Mm. intertransversarii*, but these extend back onto the sacrum, and so are not directly adjusting the ilio-sacral angle. These and other muscles of the back are drawn by Haslam (Fig. 67) and are clearly described by Nishi. Description of the ilio-lumbar muscle has caused some disagreement in the past : the accounts in the text-books of Ecker, Haslam, and Gaupp seem to have been altered by Gaupp (1896) where the ilio-lumbar muscle of *R. esculenta* is shown with a single head of origin. There is probably a specific difference here.

Rana, with a movable urostyle, has of course a coccygeo-sacral muscle, not found in *Xenopus*. This lies partly anterior to the coccygeo-iliac muscle, and partly overlaps it on the dorsal side. Indirectly, it must play an important part in ilio-sacral movements.

Movements due to excitation of muscle in R. temporaria

Method : The animal is anaesthetized under Sandoz MS. 222, beheaded, and the spinal cord is pithed. The limbs, viscera, lateral trunk musculature, the skin of the back and the *M. longissimus dorsi* are removed. A closely fitting wooden splint is inserted in the neural canal as far caudally as the sacral vertebra. The preparation is then only free to move at the ilio-sacral and coccygeo-sacral articulations. The pelvic girdle is held, projecting horizontally from supports, by a firm attachment at the acetabulum, with the dorsal side uppermost.

Electrical excitation (*cf.* Saunders & Manton, 1959) of the left and right ilio-lumbar muscles causes the vertebral column to swing upwards, rotating about the ilio-sacral joint. The end of the splint, projecting from the anterior vertebra, provides a satisfactory indicator of the arc through which the sacrum is rotating. The splint, at first inclined downwards, at 40° to 50° to the line of the ilium, swings up, on excitation, until the ilia and the splint are in line, and then further to make a reverse angle of up to 20° (i.e. a " hollow back "). This angle depends on the strength and site of excitation, the greatest effect resulting from excitation near the origin from the ilia.

Excitatation of the coccygeo-iliac muscles elicits a similar but weaker effect. Unilateral excitation of either muscle causes, in addition to the rotation in the vertical plane, an observable but slight slewing, i.e. lateral swing in the horizontal plane.

Flexing of the ilio-sacral system, as in squatting, is presumably effected by the indirect action of the belly muscles.

Demonstration of passive movement in fresh preparations

The rotation of the sacrum on the ilium can be demonstrated by substituting an iron splint for a wooden one. The vertebral column can then be passively moved, by means of a bar magnet (Plate 1, below).

The flat caudal end of the pelvis is inserted in a slit cut in a rubber stopper, which is then inserted into a stout glass tube, such as a 3 cm. diameter, 50-cc. capacity, centrifuge-tube. The tube contains frog-Ringer or Ottaway's preserving fluid. As the stopper is pressed home, its compression holds the pelvis more firmly.

In this way it can easily be seen that the sacrum will rotate on the girdle, to the extent of 25° dorsally and 25° ventrally, but through less than 5° laterally.

Similar preparations may be made of *Xenopus*. As would be expected, there is very little dorso-ventral or side-to-side movement. The sliding effect can be demonstrated with a bar magnet, by suspending an iron weight, near the bottom of the tube, from the ribs on the second vertebra. This effect is best seen on fresh preparations in frog-Ringer solution.

These demonstrations, of ilio-sacral movement in dissections, of *Rana*, show that the vertebral column is capable of rotating dorsally on the ilia through a further angle of about 40° beyond the vertebro-iliac angle of 150°–160° seen in the X-ray photographs of a " standing " frog. Such a rotation would give the appearance of a strongly hollowed back in the common frog. This appearance is not noticeable in the frog's normal walking movements, nor

I believe in any special feeding behaviour. (The back is hollow in the " Unken" defence-reflex of the " Unken " *Bombinator* sp.)

It seems probable, however, that the dorsal rotation is used in saltatory locomotion :

A. When the frog is landing, it is known to land on its forelimbs (Green, 1931, Gray, 1953). If the back and the hindlegs are straight just before landing, the forward inertia of the fore-limbs will be taken up first. Inertia of the pelvic girdle as well as the hind-limbs can be taken up subsequently through changing muscle-tonus, during the short phases of the movement when the angles at ilio-sacral, hip, knee, and ankle joints are reduced, and the hind-feet come to rest close to the fore-feet, in the squatting position.

If the back is " hollow " just before landing, the ilio-sacral articulation will be of even greater effect in absorbing inertia on landing.

B. When the frog is beginning its jump, it is at first in the squatting position. As it becomes air-borne, its hip, knee, and ankle joints open out so that thigh, lower leg, and foot are almost in the same straight line, as Gray (1953) has clearly shown. His ciné photographs seem to show a similar though slighter " opening out " of the ilio-sacral angle, so that the extensor muscles of the girdle may also assist in the jump. A more complete series of these " stills " would have to be examined before they would show whether this change in ilio-sacral angle is really taking place. But I do not think a great change in ilio-sacral angle will be shown unless the frog is leaping strongly. (See Addendum.)

In addition the change in the angle between urostyle and pelvis will be important in the jumping and landing mechanism. This has been discussed by Green (loc. cit., Fig. 16) and will not be considered here. (Green described the mechanical function of the muscle between the urostyle and the thigh, *M. pyriformis,* but not that of the coccygeo-iliac muscle.)

3. *Pelvic and sacral organization of* Discoglossus pictus

The discoglossids are usually considered phylogenetically primitive anurans (Noble, 1922, Dunlap, 1960). They are certainly less specialized in their methods of locomotion than are *Rana* and *Xenopus*. I have examined *D. pictus,* the Painted Toad, an easily available European form. This animal jumps well, swims well, and also " wriggles " well —that is, it slips through surprisingly small openings, in the manner of a toad such as *Bufo bufo*. *Discoglossus* is a fascinating animal to study.

The skeletal and muscular arrangement (Fig. 3) can be compared with that of *Xenopus*. The vertebrae are again opisthocoelous : there are three pairs of ribs, but the last pair are shorter and do not have the cartilaginous terminal plate found in *Xenopus* : the sacral vertebra has wide lateral wings but these have a *curved* distal border : the attachment of the urostyle to the sacrum is movable. The most important distincton is the presence of a well-defined joint-capsule.

The ilio-lumbar muscles, as in *Xenopus*, take origin from the anterior lateral aspect of the ilia and are directed and inserted in the same horizontal

plane. But their direction is much more oblique, so that the insertions are further from the head, on the last pair of ribs and on the fourth to sixth vertebrae. The *coccygeo-iliac muscles* are well developed and similar to those of *Xenopus*. There are, additionally, *coccygeo-sacral muscles*, like those of *Rana*.

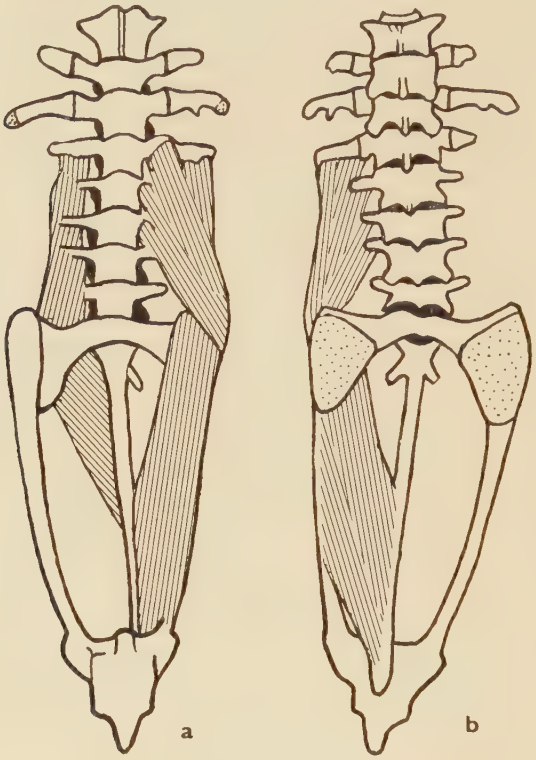


Fig. 3—Drawing, as Fig. 1, of *Discoglossus pictus* : the intertransversarial and coccygeo-sacral muscles shown on left, in 3 a.

Electrical excitation

The same procedure, using a wooden splint, is followed. As in *Xenopus*, the *ilio-lumbar muscles* act in the horizontal plane, with no observable vertical component. But the movement is lateral and not fore-and-aft ; the action of the *ilio-lumbar muscles* slews the splint through 10° to either side of the midline. The natural action of the muscle produces a slew of fully 20°, but this can only be observed when the splint is drawn forward to allow movement between the fourth to ninth vertebrae as well as at the ilio-sacral articulation.

The large *coccygeo-iliac muscles* slide the urostyle and vertebrae forwards, but the movement is very slight compared with that of *Xenopus*.

The *coccygeo-sacral muscles* produce a rotation in the vertical plane, as in *Rana*. The action causes the back to straighten until the ilio-sacral angle is almost 180°. Movement beyond this position does not occur, unlike the action in *Rana*.

Passive movement. Rotation at the ilio-sacral articulation can be effected in the vertical plane from 150° through to about 185°, which is a less extensive arc both dorsally and ventrally than in *Rana*. The sacral vertebra will also " shift forwards and backwards to some extent ", as Boulenger mentioned, but the movement is slight, as would be expected from the nature of the joint. A slewing movement of 20° to each side, with the splint in position, can be effected passively.

There is no evidence that the Painted Toad possesses extensive fore-and-aft sliding action at the articulation nor does this appear structurally possible. Yet the coccygeo-iliac muscles probably have greater importance as shock-absorbers. On landing, the head and trunk are arrested sharply, and the inertia of the still-moving hinder parts would tend to dislocate the sacro-iliac joint. In the absence of a folding movement (as in the frog) to absorb this shock, the *Mm. coccygeo-iliaci* can perform a similar elastic function.

Function of the ilio-sacral articulation in Discoglossus

Observation of living Painted Toads shows that vertical movement at the articulation is less than in *Rana*, as would be expected from the dissected material. In side-view the back remains curved, whether sitting or standing, not sharply angled, nor straight, as in *Rana*. X-ray photographs show that this is partly due to a smaller ilio-sacral movement (Plate 2, D).

The Painted Toad jumps well, but probably lands less smoothly than the Common Toad. This would make successive jumps, on land, more difficult, but the Painted Toad is more aquatic in its habitat through the year.

The lateral swing (slewing) which is found in *Discoglossus* is an advantage to an animal that seizes its food with its jaws and not with its tongue. *Discoglossus* is extraordinarily agile in this respect ; in a single lateral flexure it has been seen to snap up food lying in contact with one of its hind feet.

CONCLUSIONS

It has been shown that considerable movement occurs at the ilio-sacral articulation, in three anurans of different habits, and of contrasting skeletal structure. From the published figures of anuran osteology, most anuran ilio-sacral skeletal systems appear to correspond to one or other of the types studied, or to be intermediate forms. The action of the joint may also accord, in anurans generally, with one of the three types of movement described here, since these types include the main theoretical possibilities —lateral bending, vertical bending, and longitudinal sliding actions. Beddard (1907, 1908, 1911) has described several species where the muscles of the ilium sacrum and urostyle were unusual, but these variations in the muscular apparatus belong, so far as can be seen from his figures, to one of the types described here.

Therefore *the movements described and the structural systems on which they depend probably occur generally in Anurans.* These movements may well have been evolved independently in different phylogenetic lines of Anura. There may also be considerable movement at the articulation in urodeles, where the connection of the pelvis is also to one sacral vertebra. It is only in the Amniotes, lacking an aquatic larval stage with no ilio-sacral articulation,

and having a pelvis connecting to two or more sacral vertebrae in the adult, that a movable joint is no longer to be expected. (Even in Amniotes, a slight movement occurs. Young 1957.)

There is strong evidence that the ilio-sacral movements, and the muscles producing them, are an integral part of Anuran locomotion. In *Discoglossus*, the *coccygeo-iliac muscles* appear to be an essential shock-absorber during saltation. The *ilio-lumbar muscles* are an important part of the mechanism by which a Painted Toad can slew its body on its back legs, either as it moves to seize its food, or when escaping, as it slips with agility through crevices.

In *Rana*, the ilio-lumbar and *coccygeo-iliac muscles* appear to act interdependently with the coccygeo-sacral muscle. The action is an extensive, but delicately adjusted, rotation of the trunk on the pelvis, chiefly in a vertical plane. It is very probably an important part of the jumping and landing mechanism. This condition may well have been derived from a more generalized one in animals such as *Discoglossus*, after the tongue had become the main food-securing device and extensive lateral trunk-slewing movements were no longer so important. (The leiopelmids, which might be more nearly related to a common ancestor of the Anura, have not been examined ; illustrations of the pelvis and sacrum of *Ascaphus* suggest a form intermediate between *Rana* and *Discoglossus*.)

In *Xenopus*, Palmer has shown that the *ilio-lumbar* and *coccygeo-iliac muscles* act antagonistically in retracting and projecting the vertebral unit upon the pelvis, and that the resulting change in length can occur to its full extent in locomotion when the hind-feet are pushing *against a solid surface.*

Now *Xenopus* is purely an aquatic form. Under natural conditions it swims, or it burrows in sub-aquatic mud. In mud, an alternate lengthening and shortening of the trunk would serve to bring the powerful hind-limbs further forward at the beginning of each stroke and thereby would lengthen the distance achieved by each cycle of hind-limb movement.

An adaptation of this sort would be an advantage for burrowing Anura, even, presumably, where they burrow backwards into the substratum. The adaptation involves broad sacral diapophyses, with a *straight* distal edge where the sliding contact with the ilia occurs, and a *fixed* attachment of the urostyle for the " coccygeal " muscles. It is perhaps significant that, in all the European Anura, illustrated by Boulenger, these two modifications appear only once—in *Pelobates fuscus*, the " essentially fossorial " Spadefoot Toad.

ACKNOWLEDGMENTS

I wish to thank Dr R. N. Smith for taking the X-ray photographs, and Miss B. Passaway and Miss G. Styles who also took part in this. I acknowledge with pleasure the work of Mrs Margaret Palmer, from whose studies this further work developed, and the helpful criticism of Professor J. E. Harris and Mr J. F. Sloane, and the technical help of Mr G. L. E. Wing, Mr N. Ablett and Mr K. Wood.

ADDENDUM

After the session in which this paper was given, Miss C. L. T. Lucas, Department of Biology, Royal Free Hospital School, London, mentioned that

Fig. 4—Tracings of photographs of a single leap of *Rana catesbiana*, from the stroboscopic photographs of Mr Earl Edmiston, Angels Camp, California.

she possessed some photographs which she thought gave support to my conclusion. She most kindly lent them to me. They give the evidence that was needed, a study of a frog leaping strongly—" The jumping frogs of Calaveras " in fact (Twain, M. 1867!).

The photographs were sent from Angels Camp, California, by Carl T. Mills, who organized the world jumping contests of frogs there, and most kindly gave me permission to use them. They form a series of twelve stroboscopic photographs, showing a single leap of a Bull-Frog, *R. catesbiana*. The photographer was Mr Earl Edmiston, of Angels Camp. Some of the photographs were published by Dr M. Burton in the *The Illustrated London News*, May 16th, 1953.

This information is included as Fig. 4. In the light of p. 51 it needs no comment. I am most grateful to Miss Lucas.

REFERENCES

Barclay, O. R. (1946). The mechanics of amphibian locomotion. *J. exp. Biol.*, **23** : 177

Beddard, F. E. (1895). On some points in the anatomy of *Pipa americana*. *Proc. zool. Soc. Lond.* **1895** : 827.

Beddard, F. E. (1895). On the diaphragm and the muscular anatomy of *Xenopus*, with remarks on its affinities. *Proc. zool. Soc. Lond.* **1895** : 841.

Beddard, F. E. (1907). Notes upon the anatomy of a species of frog of the genus *Megalophrys*, with references to other genera of Batrachia. *Proc. zool. Soc. Lond.* **1907** : 324.

Beddard, F. E. (1907). A contribution to the knowledge of the batrachian *Rhinoderma darwini*. *Proc. zool. Soc. Lond.* **1907** : 678.

Beddard, F. E. (1908). On the musculature and other points in the anatomy of the *Engystomatid* frog *Breviceps verrucosus*. *Proc. zool. Soc. Lond.* **1908** : 11.

Boulenger, G. A. (1896). *Tailless batrachians of Europe*. London.

Burton, M. (1953). Jumping frogs. *Illustrated London News* (16th May, 1953).

Dunlap, D. D. (1960). The comparative myology of the pelvic appendage in the Salientia. *J. Morph.* **106** : 1.

Gadow, H. (1901). *Amphibia and reptiles*. (Cambridge Natural History). London.

Gaupp, E. (1896). Der seitliche Bauchmuskeln der anuren Amphibien. *Anat. Anz.* **11** : 745.

Gray, J. (1953). *How animals move*. Cambridge.

Green, T. L. (1931). On the pelvis of the Anura : a study in adaptation and recapitulation. *Proc. zool. Soc. Lond.* **1931** : 1259.

Gregory, W. K. (1935). The pelvis from fish to man : a study in palaeomorphology. *Amer. Nat.* **69** : 191.

Grobelaar, C. S. (1924). Beitrage zu einer Monographie von *Xenopus laevis* (Daud.) *Z. ges. Anat.* (Abt. 1). *Z. Anat. EntwGesch.* **72** : 131.

Haslam, G. (1889). *Ecker's Anatomy of the frog*. Oxford.

Howell, A. B. (1944). *Speed in animals*. Chicago.

Keith, A. (1905). The nature of the mammalian diaphragm and pleural cavities. *J. Anat., Lond.* **39** : 243.

Marshall, A. M. (1928). *The frog*. London (12th Ed.).

Millard, N. (1941). The vascular anatomy of *Xenopus laevis* (Daudin). *Trans. roy. Soc. S. Afr.* **28** : 387.

Mookerjee, H. K. (1931). On the development of the vertebral column of the Anura. *Phil. Trans. roy. Soc.* B **219** : 165.

Nauck, E. T. (1938). *Handb. vergl. Anat. Wirbelt.* (Bolk *et al.*). Berlin.

Nishi, S. (1938). *Handb. vergl. Anat. Wirbelt.* (Bolk *et al.*). Berlin.

Noble, G. K. (1922). The phylogeny of the Salientia. 1. The osteology and the thigh musculature ; their bearing on classification and phylogeny. *Bull. Amer. Mus. nat. Hist.* **46** : 1.

Noble, G. K. (1931). *Biology of the Amphibia.* New York.
Palmer, M. (1960). Expanded ilio-sacral joint in the toad, *Xenopus laevis. Nature, Lond.* **187** : 797.
Parker, H. W. (1932). Parallel modifications in the skeleton of the Amphibia Salientia. *Arch. Zool., Torino* **16** : 1240.
Passaway, B. (1960). Personal communication.
Ridewood, W. G. (1897). On the development of the vertebral column in *Pipa* and *Xenopus. Anat. Anz.* **13** : 359.
Ritland, R. M. (1955). Studies on the post-cranial morphology of *Ascaphus truei. J. Morph.* **97** : 119 and 215.
Saunders, J. T. & Manton, S. M. (1959). *Practical vertebrate morphology.* London (3rd Ed.).
Twain, M. (1867). *The celebrated jumping frog of Calaveras County and other sketches.* New York.
Young, J. Z. (1957). *The life of mammals.* Oxford.

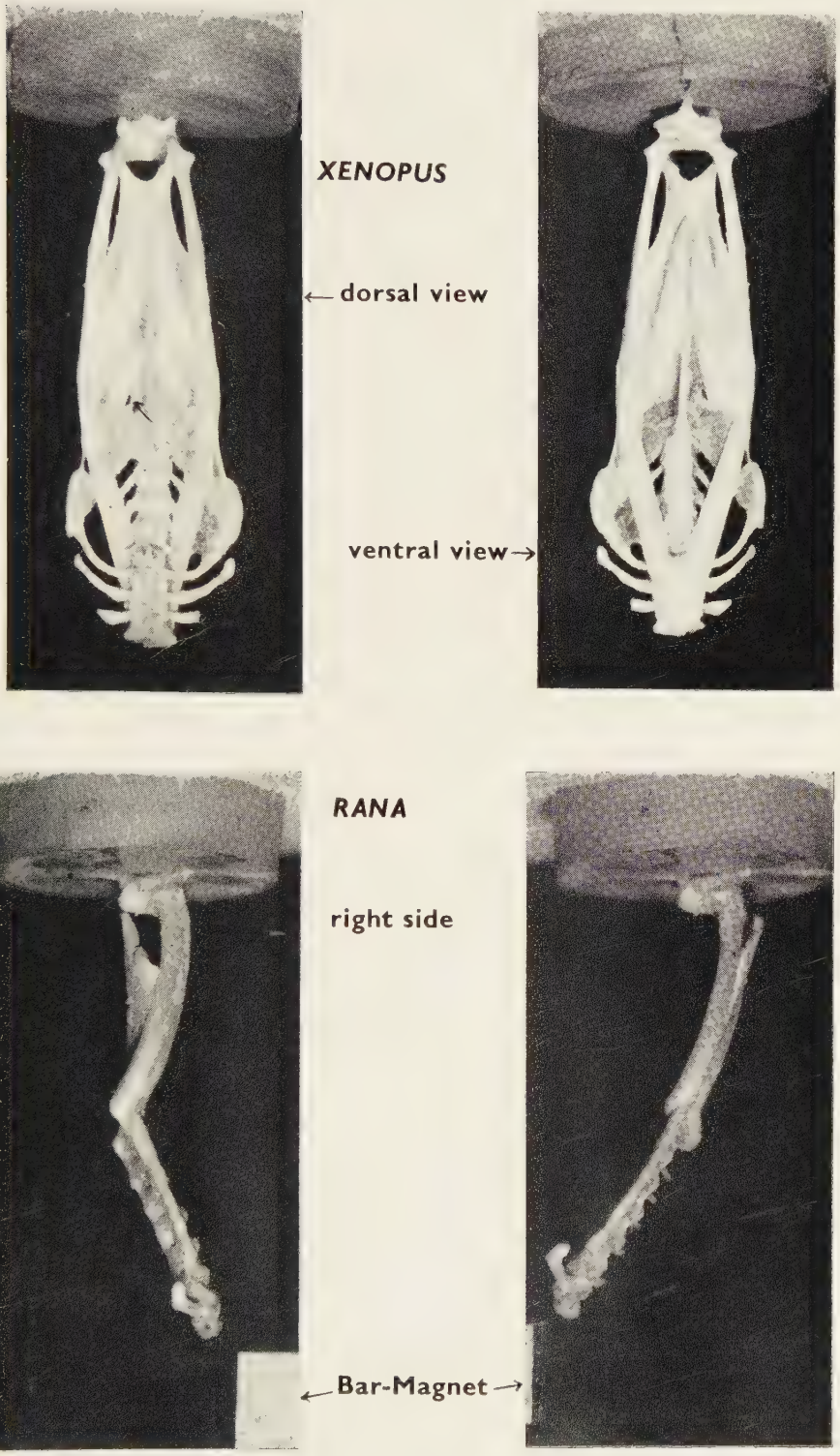
GENERAL DISCUSSION

Chairman : Professor Sir James Gray, C.B.E., F.R.S.

Dr Savage : If *Xenopus* are kept in an aquarium with underwater shelters they come up to breathe at intervals by extending their bodies slowly towards the surface, where they breathe heavily for a minute or so and then retract with a sudden movement into their shelters again. This movement is exactly the kind of thing which Dr Whiting describes. In *Pelobates*, there is an interesting stage in the burrowing behaviour. The animal sinks into the ground by using its spades and stays there. At intervals the loose soil behind the animal is shoved forwards by the hind feet over the back of the animal from behind forwards ; I had always related this motion to the peculiar position of the hind limbs, but this may be another function of the sliding joint in *Pelobates*.

Dr Walker : When a frog jumps, because of this possibility of rotation between the pelvic girdle and the vertebrae, there must be a strong tendency for the body to flex and sway. The muscles on the dorsal side could function as a shock absorber to keep the body on an even keel.

Dr Whiting : T. L. Green made this same point a long time ago with particular reference to the coccyx and his argument would have even greater force if the pelvis is taken into consideration as well.



Dissections of *Xenopus* (above) and *Rana* (below), mounted to show movements at the ilio-sacral joint. They were removed from the glass vessels before being photographed. In the dorsal view of *Xenopus* a black arrow indicates the anterior edge of the lumbodorsal fascial band. *Rana* dissections are shown in lateral view, with the magnet in position (the urostyle has rotated in the photograph more than it could in the living animal).

X-ray photographs of *Rana temporaria* (R) and *Discoglossus pictus* (D).

LOCOMOTION OF SEALS WITH PARTICULAR REFERENCE TO THE FORELIMB

BY

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The patterns of terrestrial and aquatic locomotion in the grey seal (*Halichoerus grypus*) and certain other species of Phocidae are described. Particular reference is made to the forelimb, which in certain species is subjected to a very wide range of extremely powerful movement patterns. Certain specializations, particularly of the muscular system, which are directly related to these movement patterns, are described.

CONTENTS

	Page
Introduction	59
Aquatic locomotion	60
Terrestrial locomotion	62
Patterns of forelimb function	65
Features of forelimb anatomy	65
Discussion	71
Summary	74
Acknowledgments	75
References	75
General discussion	75

INTRODUCTION

The three families of Pinnipedia each display major differences in locomotion despite similarities in natural history. These locomotor differences represent one facet of the evidence for believing that the Phocidae and Otariidae, if not the Odobenidae, have different evolutionary stems. All three families display the " fin feet " characteristic of the order. These feet have many anatomical similarities, but also exhibit major anatomical and functional differences. On land the Otariidae and Phocidae both have, in the forelimbs, the metacarpophalangeal hyperextension and interphalangeal flexion when weight bearing, which is so characteristic of the Carnivora, in spite of the fin development, but these limbs are used quite differently in the two families.

At sea the walrus swims with a curious combination of lateral and true flexion at its hind end, the hind-flippers providing the main propulsion but assisted by the fore-flippers as paddles. Those Otariidae, which have been observed, swim by means of a sculling motion of the fore-flippers occasionally assisted in certain species, e.g. *Zalophus californianus* by side-to-side sweeps of the hind-flippers, particularly when accelerating or swimming at maximal speed : a young specimen of *Callorhinus ursinus* however, was never observed to use its hind-flippers. The walrus can perhaps be discounted when con-

sidering high speed at sea. The majority of otariids do require to swim rapidly, yet, considering that the most effective driving thrust should come from the hind end, a contention amply illustrated by most other high speed aquatic animals, it appears somewhat strange that this group should have developed towards a forelimb form of aquatic propulsion. Of the Pinnipedia only the Phocidae have taken the apparently logical step of leaving the dog or bear paddle behind and evolving in a way showing comparison with such truly marine mammals as the Cetacea and the Sirenia. The Phocidae have evolved towards an efficient hind end marine propulsion, using their large, webbed, fish-tail like hind-flippers rather than a tail. The price of this advanced aquatic specialization is high, however, when the seal is land-based, as it must be during the breeding, and in some species, moulting seasons.

When ashore the other two families of Pinnipedia can maintain some degree of quadrupedal gait, but the Phocidae have lost the use of their hind limbs which are permanently directed backwards. Thus the seals have evolved not only a characteristic locomotor efficiency at sea (only the sea otter is really comparable), but they have gone so far along this line that they have developed a completely new form of progression ashore.

Morphological and functional observations have been made on the grey seal (*Halichoerus grypus*), common seal (*Phoca vitulina*) and elephant seal (*Mirounga leonina*) with some observations on living specimens only of the Greenland seal (*Phoca groenlandica*), ringed seal (*Pusa hispida*) and Baikal seal (*Pusa sibirica*). Cine film of locomotion has been made mainly on the grey seal, both at standard and high (180 frames/second) speeds.

AQUATIC LOCOMOTION

Seals exhibit a wider range of locomotor patterns at sea than the more highly specialized Cetacea and Sirenia, but nevertheless there is a basic method with several lesser used variations. When swimming quickly, the hind-limbs provide the propulsive force. The thorax is carried relatively rigidly, forming a compact unit with the neck and head (though the neck may be bent in one direction when the animal changes direction). Based on this fixed unit the hind part of the animal is swept from side to side, the lateral flexion being maximal in the lumbar region. The hind limbs with their short shank and greatly expanded fish-tail like feet are used alternately to strike the water with the volar surface. As the pelvis swings towards the right, the right limb is maintained in flexion and the left limb extended to provide the drive. At the end of the stroke the left limb flexes, and, as the pelvis begins to move towards the left, the right foot opens to take over the drive. The seal thus swims in a manner sometimes considered somewhat fish like, but complicated by the double limbs, the flexed limb leading the move active at all times, and thus producing considerable disturbance ahead of the driving limb. Such disturbance might be considered to reduce efficiency, but in spite of this, seals can swim quite quickly, i.e. well over ten miles per hour, though not quite in the same class as porpoises and dolphins of comparable size.

Seals sometimes swim with the hind limbs placed together, with volar surfaces in contact, thus forming a single fish-tail like unit, but this method

has not been observed in animals swimming at speed. It appears less efficient in practice than the more usual method. A third method of hind limb propulsion is sometimes seen : the two hind limbs are abducted in flexion, and adducted in extension, the large feet being driven volar surfaces together. A seal may sometimes use this method in rapid acceleration, and then switch over to normal swimming; it is never maintained for more than a few strokes.

The fore-flippers play a relatively inactive role when a seal is swimming on a steady course. They lie flat against the body wall, directed caudalwards in a somewhat extended axillary hollow in the body fat. In this way they

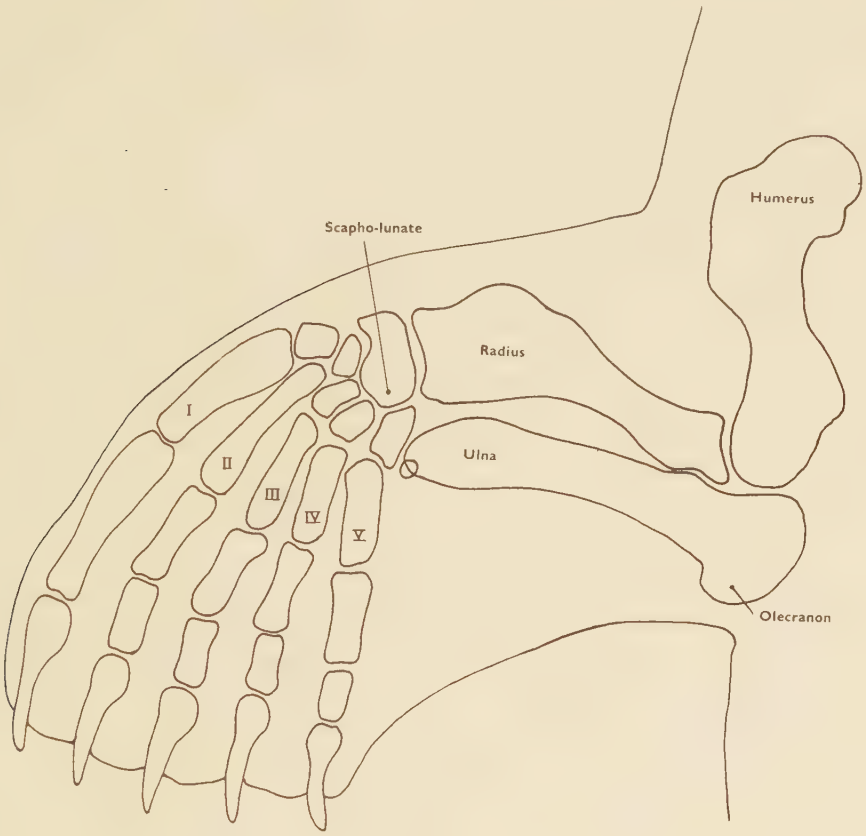

Fig. 1—Tracing showing forelimb borders and bones from a radiograph of a young grey seal. The limb is in ulnar deviation and the course of the abductor digiti minimi muscle from the olecranon tip to the intermediate phalanx of the fifth digit can be seen.

project relatively little above the body surface, follow the body lines reasonably closely, and so produce minimal disorganization of the seal's streamline form. Even the hairs of the limb follow those of the body wall quite closely. When the seal changes direction, the fore-flippers play a more active role, being used basically either as hydroplanes, comparable with the fore-flippers of Cetacea, or as paddles, this latter usually being the role of the outside flipper to give extra thrust on the periphery of the turning circle. When a seal is swimming

slowly, when fishing inshore among rocks, or maintaining its position at the surface on observation, or asleep, the fore-limbs may be used as paddles, the hind-limbs being held still, or used only to a small extent.

Two main patterns of active movement are therefore required of the fore-limb in swimming :

(1) It is carried with the forearm and manus projecting from the body surface, the limb in a mid-prone-supine position, the joints distal to the elbow firmly extended, and the manus in marked ulnar deviation. A hydroplane is thus formed, with a thick crescentic leading edge made up of the heavy radius and radial digit. The forearm skeleton fills only the leading two-thirds of the limb, the trailing edge between the body wall and the ulnar digit being made up of a tough elastic fold of skin which stretches from the prominent olecranon process at the body wall across to the digitus minimus and containing a bundle of muscle in its free edge (Plate 1 and Fig. 1). The backwardly directed (ulnar deviated) manus makes up the lateral part of the hydroplane. The seal's short fore-limb thus forms a hydroplane of excellent hydrodynamic form. The marked ulnar deviation shortens the total lateral length of the limb, but nevertheless the surface area is increased by the ulnar fold of skin. By this means the resultant of the total lift on the flipper, which is directly related to surface area, is brought nearer to the centre of the body, thereby reducing the intrinsic strength of forearm structures required to withstand the bending moment. By reducing the limb's effective length, the muscles employed, especially on the ulnar border, obtain better leverage. This short crescentic shape also makes the limb better able to withstand the marked pressure changes associated with high speed swimming in rough, and especially inshore, waters and also allows easy clearance of obstacles.

(2) When used as a paddle the manus is carried forwards with elbow flexion. The manus is extended in pronation and then pulled backwards, the elbow extending, with final wrist and digital flexion at the end of the stroke. The digits are spread so as to give maximum width to the paddle. A simple flexion and extension of the joints of the limb with pronation of the forearm are therefore required : the whole movement is rather like the movement of the arm in the human breast stroke.

TERRESTRIAL LOCOMOTION

On land the seal must move without the use of its hind limbs. This is accomplished by a peculiar hitching forward of the trunk which Matthews (1952) described as resembling the movement of a looper caterpillar. The sternum and the pubis are used as the main weight bearing points and progression levers. Extending the head and neck, as much weight as possible is carried well forward and the hind part of the body is raised from the ground. the whole weight of the animal being taken and balanced on the sternum. The trunk is then markedly flexed caudal to the sternum so that the pubis is brought forward well in advance to its original position and replaced on the ground. Thrusting with the pubis the trunk is rapidly extended and the fore part of the body thrown forward. The seal thus advances with a series of flexor/extensor movements of the trunk based on the weight bearing sternum

and the driving pubis, but being dependent upon the heavy and extensible head and neck, which can thus balance the weight of the animal behind the sternum, so allowing it to lift its hind part and hold it clear of the ground. If a seal wishes to turn it raises its fore and hind parts from the ground and pivots on its sternum. By this means a seal can progress quite quickly without even using its forelimbs. Animals can often be seen crossing smooth sand or a smooth surface, where the forelimbs could not get a grip, by simple body hitches, the forelimbs being carried extended and abducted to the side and raised clear of the ground. Those seals such as the grey seal (*Halichoerus grypus*) which often traverse firm less smooth ground, rocks, pebble or boulder beaches, or even climb quite steep slopes, make considerable use of the forelimbs whenever possible. Even when traversing smooth or sandy surfaces the grey seal will often use its flippers if in a hurry.

The limb being small, a condition accentuated by the bulky body, it can only be effective in terrestrial locomotion if weight bearing be maintained well distalwards. In common with many other Carnivora, seals bear the weight primarily on the metacarpal heads, a practice made possible by a considerable degree of metacarpophalangeal hyperextension and a concurrent interphalangeal flexion which brings the claws to the ground. When the limb is used in progression, the metacarpophalangeal hyperextension and interphalangeal flexion becomes more marked so that, although the weight is taken on the metacarpal heads, the long claws attached to the terminal phalanges strike the ground practically at right angles : the limb is thus a weight bearing instrument equipped with a powerful terminal hook (Fig. 2 and Plate 2).

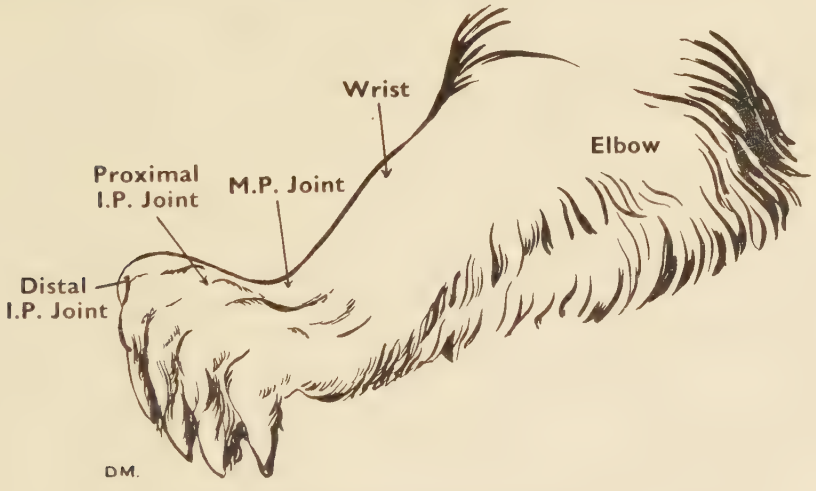

Fig. 2—Drawing to illustrate the forelimb haulage grip of a grey seal.

A new-born grey seal will drag itself along using its forelimbs alternately, but from the time it is four to five days old the forelimbs are used together. They are carried forward and hooked into the ground, level with the fore part of the neck, so that by pulling them back and taking the weight on the metacarpal heads, the sternum is raised from the ground and the body dragged

forwards. Meanwhile the trunk is flexed, bringing the pelvis well forward, and then extended with powerful drive from the pubis. As the body moves ahead of the fore limb support, the thrust from the pelvis is assisted by a final metacarpophalangeal flexion, and a remarkable degree of ulnar deviation which throws the body forward onto the sternum. The limbs are

Fig. 3—Diagram of forelimb haulage in a young grey seal drawn from frames of a cine film.

then carried forward and the process repeated (Fig. 3). When moving quickly, the seal may drive off with the foreflippers before the pubis reaches the ground, so that the whole weight of the animal is thrown forward by the forelimbs and the drive then taken up by the pubis in quite a smooth sequence. This form of progression is ungainly, the animal bouncing on its belly in a way which induces large shock waves in the blubber, but nevertheless a seal can travel at six to eight miles per hour over short distances. Seals are even capable of remarkable climbing feats. If a seal can maintain an adequate friction grip with its pelvis (which is assisted by the hard caudally directed hair) and flipper grips even in front of its head, it can climb slopes of 60° or more. One cow seal in an effort to escape to the sea dashed at a large roughly cubical block with a flat face angled at between 70° and 80°, and " leaped " at this so that the forelimbs were hooked over the crest a little ahead of the nose, and the hind flippers just clear of the ground, taking virtually the whole weight on the terminal phalanges hooked over the top. The seal gradually heaved herself up until the sternum was level with the top ridge and then tipped over and down the other side. Such examples amply illustrate the tremendous power of the haulage grip.

The pattern of metacarpophalangeal hyperextension with interphalangeal flexion is used by the seal for many of its day-to-day activities, e.g. feeding.

Seals can often be seen holding food such as cephalopods, bony fish, etc., by a two-handed terminal interphalangeal grip, eating the desired parts, and throwing the rest away. This grip is extremely powerful even in extreme interphalangeal flexion. A single human finger can be held firmly and even hurt when squeezed between the seal's terminal and intermediate phalanges.

PATTERNS OF FORELIMB FUNCTION

The seal forelimb is thus remarkable in that it is required to carry out a wide range of very different movement patterns, probably more than any other animal with the possible exception of Man. The manus is capable of :— (1) being held in extension sufficiently rigid to withstand considerable pressure variations as a hydroplane at sea ; (2) complete and powerful flexion when used either as a paddle or at the terminal phase of terrestrial locomotion ; (3) maintaining a metacarpophalangeal hyperextension coupled with an extremely powerful interphalangeal flexion, even when weight bearing on the metacarpophalangeal heads ; (4) imparting a powerful ulnar deviation not only at the wrist and carpal joints, but also at the metacarpophalangeal joints, at the same time as all the above flexion-extension patterns are in use ; (5) maintaining adequate radial control so as to present a stable edge to the sea as a hydroplane. These patterns of movement control are reflected in the skeletal and muscular systems of the forelimb.

But in spite of this wide range of powerful movement required of the limb it is remarkable how free are its overall movements. As an example seals are able to scratch areas within the length range of the limb with greater ease even than Man. An elephant seal was observed to scratch an area over the scapular region of the back. Using both limbs on different occasions over several minutes, and with the same limb turned caudally (i.e. extended) and cranially (flexed) to bring the digits to the back to scratch, all with apparent ease : this could not have been accomplished by a human for all the human freedom of forearm movement.

FORELIMB ANATOMY

The anatomy of the seal forelimb has been described extensively by Duvernoy (1822), Humphry (1868), Murie (1870), Lucae (1872), Miller (1887) and Howell (1929), and the relationship of anatomy to function further discussed by Howell (1930). Howell's observations of the limb in use were obviously very few so that his conclusions are based on shrewd attempts at arguing from anatomy to function rather than from combined observations. He considered that the forelimb played little or no part in locomotion, and was therefore unable to understand the reasons for the specializations he found.

There is no reason to reiterate anatomy already well described but only to point out variations, particularly from Howell's complete descriptions, and such factors as are of major importance in considering the specific locomotor specialisations.

The general foreshortening of the limb is well understood, but although length is reduced the bones maintain their thickness. Despite the better leverage offered to muscles by bone shortening there is a considerable development of such features as the deltoid and greater and lesser tuberosities of the

humerus, the medial and lateral humeral condyles, an enormous olecranon and an extremely prominent preaxial border of the lower end of the radius, which is well in advance of the carpals (Fig. 1). There is also a marked flattening of the antebrachial skeleton, which is co-extensive with the large flat manus. Howell argues that the large deltoid and greater and lesser tuberosities are probably associated with such structures as the large cephalo-humeral muscle acting upon the head, but fully as important are the powerful humeral movements, among which rotation is of necessity very powerful, and controlled by powerful *subscapularis* and *infraspinatus* muscles, so necessary when the limb acts as a hydroplane.

The large flattened olecranon gives insertion on the one hand to an enormous triceps muscle, but also origin at its tip to such important muscles as *abductor digiti minimi longus*, and *flexor carpi ulnaris*, both of which benefit from the prominence of origin on the postaxial border of the limb. The large ridged preaxial border of the lower end of the radius has been described by Howell as a *pronator teres* ridge, but such a name is obviously unsatisfactory since *pronator teres* is inserted short of the apex of the ridge. This ridge emphasizes the curvature of the leading edge of the hydroplane which then falls away laterally into the manus, and, being deeply grooved by *abductor pollicis longus* (*extensor metacarpi pollicis*) gives increased leverage to this muscle in its approach to the first metacarpal.

The wrist joint is of particular interest, for this joint together with the mid-carpal and carpo-metacarpal joints subserves a variety of functions. The scapholunate bone which articulates with the lower end of the radius (Plate 3) has a somewhat triangular articular surface, being relatively narrow on the postaxial side and broad preaxially. Dorsally it has a very prominent preaxial ridge with a smaller ridge ventral to a concave surface whilst the two convexities are confluent with a convex postaxial surface : the effect is thus a " V " shaped convexity. The concave preaxial surface (the hollow of the " V ") fits a prominent preaxial ridge on the radius with the dorsal scapholunar ridge lying in a hollow of the radius. This arrangement gives an extremely stable joint which allows no antro-posterior sliding when the manus is in the radio-ulnar plane, a point of importance when the manus is used as a relatively rigid hydroplane. In flexion however, the scapholunar ridge is carried up onto the radial ridge thus producing marked ulnar deviation.

Although there is a considerable amount of interdigitation between the carpal bones of the two rows, thereby giving stability, there is still free extensor-flexor movement and deviation, particularly in an ulnar direction. This deviation is also an important feature of the carpo-metacarpal joints where some spreading of the digits is possible (a function of this rather more than the metacarpophalangeal joints). The base of the fifth digit is well slotted into the carpus for stability, but the digit is free to move considerably in a postaxial direction, a movement which can be followed by the other metacarpals.

The locomotor patterns of the seal are extensively reflected in the muscular system. The proximal musculature shows few special modifications other than shortness of length, but is of considerable bulk and power. Howell

found this tremendous size rather surprising, causing him to wonder if in fact the limb was used as little as he thought. So large is the triceps that it is inserted not only into the olecranon, but also some half way along the ulna. However the most marked specializations are found in the antebrachium and manus.

The musculature of the antebrachium is covered by an extremely dense, deep, investing fascia, but two muscles, *palmaris longus* and *abductor digiti minimi longus* (*abductor digiti quinti longus*) lie superficial to this fascia, both

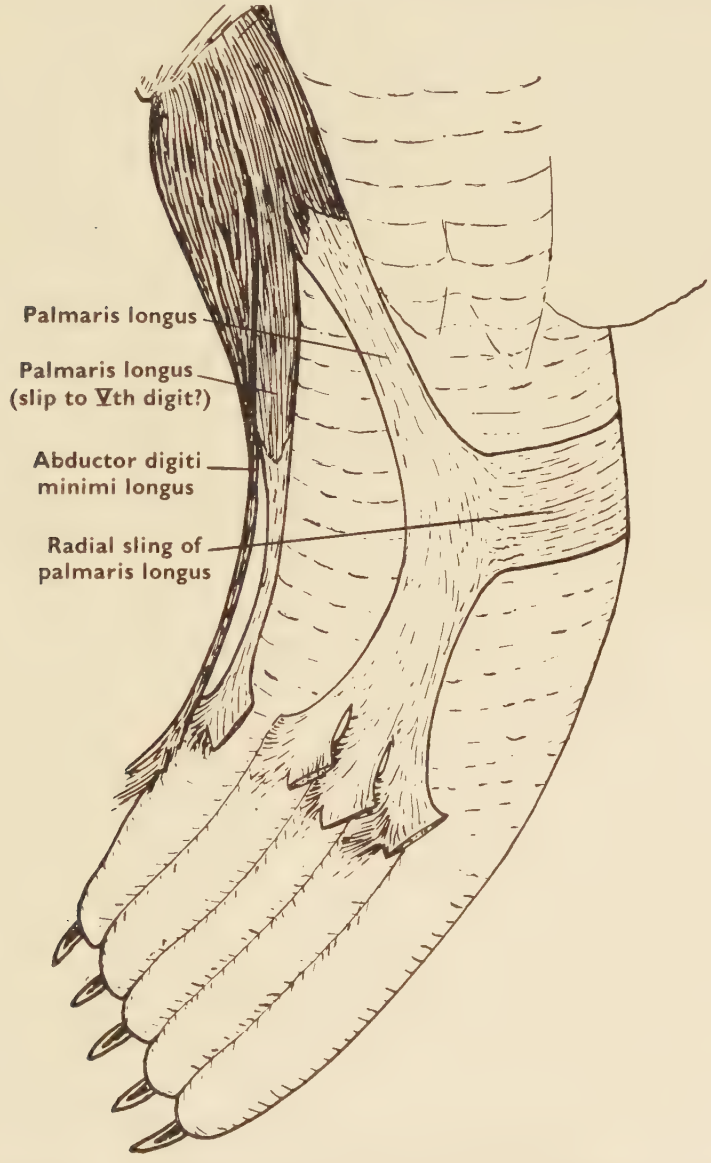

Fig. 4—Illustration of the superficial flexor musculature of the volar aspect of the distal part of a grey seal forelimb.

arising from the olecranon (Fig. 4). *Palmaris longus* runs along the flexor aspect of the limb forming a flat tendon, which is slung by a broad flat fibrous sheet to the preaxial border of the radius. From this point the tendon swings into the line of the manus to be inserted into the fibrous flexor sheaths of the intermediate three digits level with the bases of the proximal phalanges and into the overlying skin. A further somewhat variable segment usually runs to the fifth digit in a like manner, but without a preaxial sling.

Abductor digiti minimi longus arises from the postaxial tip of the olecranon more or less confluent in origin with *palmaris longus*. It runs distalwards in the free border of the post-axial fold of skin (Plate 1B) forming a rounded tendon and giving an insertion into the post-axial side of the fifth digit—mainly into the intermediate phalanx and the overlying skin. This muscle can be felt contracting in a living animal, in the post-axial fold of the skin, producing post-axial deviation of the manus and at the same time, by bow-stringing subcutaneously across the fold, pulling this elastic skin away from the ulnar and forming a relatively thin, but elastic trailing edge to the hydroplane.

The remainder of the antebrachial musculature lies deep to the dense investing fascia. On the flexor side two muscles are of especial interest : *flexor digitorum communis* and *flexor carpi ulnaris* (Fig. 5).

Flexor digitorum communis is a large muscle which is a combination of *flexores digitorum profundus, sublimis et pollicis longus.* Although it arises from three separate heads of origin on the medial humeral epicondyle, the medial side of the olecranon and upper three-quarters of the volar surface of the ulnar, and from the intermediate one-third of the volar surface of the radius and the interossious ligament, all the fibres join together to form a single but extensive, fleshy belly. Three thin muscle bellies, *flexor digitorum sublimis* leave the ventral aspect, whilst the remainder runs on to form a thick flat combined tendon of *flexores digitorum profundus et pollicis longus.* The very small *flexor digitorum sublimis* gives three thin tendons which gain a typical insertion into the intermediate phalanges of the second, third and fourth digits. Each tendon receives a thin tendinous addition from *palmaris longus* on its ulnar side over the proximal phalanx. The thick tendon of the combined muscle continues over the carpal region where it divides into five tendons, a lateral *flexor pollicis longus*, and four medial, *flexor digitorum profundus.* These tendons pass through the carpal tunnel formed by *flexor carpi ulnaris* and are inserted into the terminal phalanges. Only one tendon, that to the first digit, gives origin to a lumbrical muscle which runs into the post-axial side of the extensor expansion of the first digit.

Flexor carpi ulnaris is a most remarkable muscle being far larger than *flexor carpi radialis* and practically as large as the combined *flexor digitorum communis.* It arises from the olecranon and the shaft of the ulna, and over the distal third of the ulna forms a thick tendon, which, before reaching the pisiform bone divides into two approximately equal parts. The ulnar portion runs into the pisiform bone and thence by a deep tendon to the base of the fifth metacarpal bone and a superficial tendon which splits to run into the fifth, fourth and sometimes the third proximal phalanges. The other large

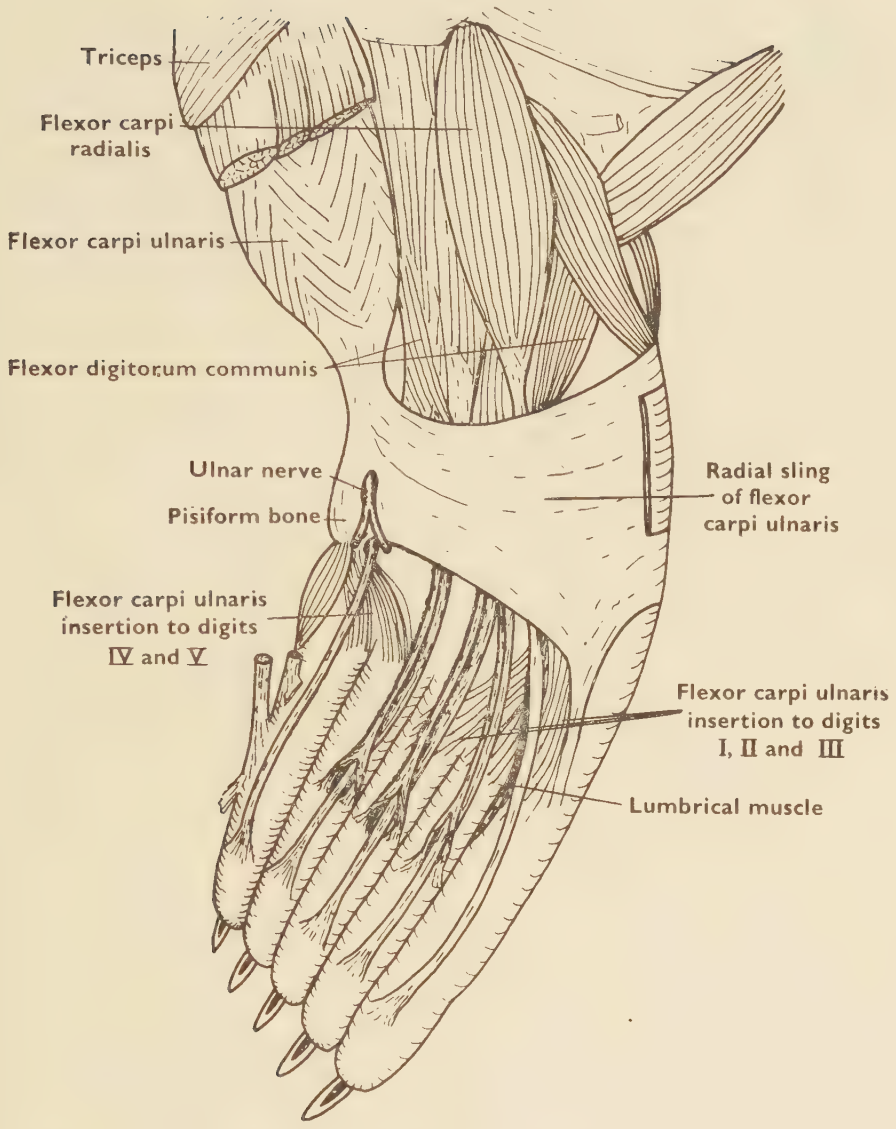
Triceps
Flexor carpi radialis
Flexor carpi ulnaris
Flexor digitorum communis
Ulnar nerve
Pisiform bone
Radial sling of flexor carpi ulnaris
Flexor carpi ulnaris insertion to digits IV and V
Flexor carpi ulnaris insertion to digits I, II and III
Lumbrical muscle

Fig. 5—Deep structures of the volar aspect of the distal part of a grey seal forelimb.

division runs to the distal end of the radius where its superficial fibres gain a wide insertion into the pre-axial border of the limb from the lower end of the radius to the base of the first metacarpal, deep to, and comparable with, the retinacular fibres of *palmaris longus*. The deeper fibres form three thickenings under the aponeurosis and wind around the pre-axial aspect of the *flexor digitorum communis* tendons and then, running deep, gain insertion into the ventral aspect of the first, second and third proximal phalanges. *Flexor carpi ulnaris* thus acts as a flexor of the metacarpophalangeal joints as well as its usual function of a flexor-ulnar deviator at the wrist.

The seal has two long extensor muscles to the digits, as do many other carnivores, e.g. the otters, and bedevilled by a variety of names (Fig. 6). The deeper of these is the larger and more powerful and sends four tendons towards the postaxial sides of the second to fifth digits. Over the metacarpal heads they fan out to form an extensor expansion comparable with that of *extensor digitorum communis* of Man. Within this extensor expansion fibres run along the digit mainly on the postaxial side to the intermediate and distal phalanges. This muscle is essentially the extensor at the metacarpophalangeal joints. The superficial muscle runs distalwards as a single flattened tendon and only

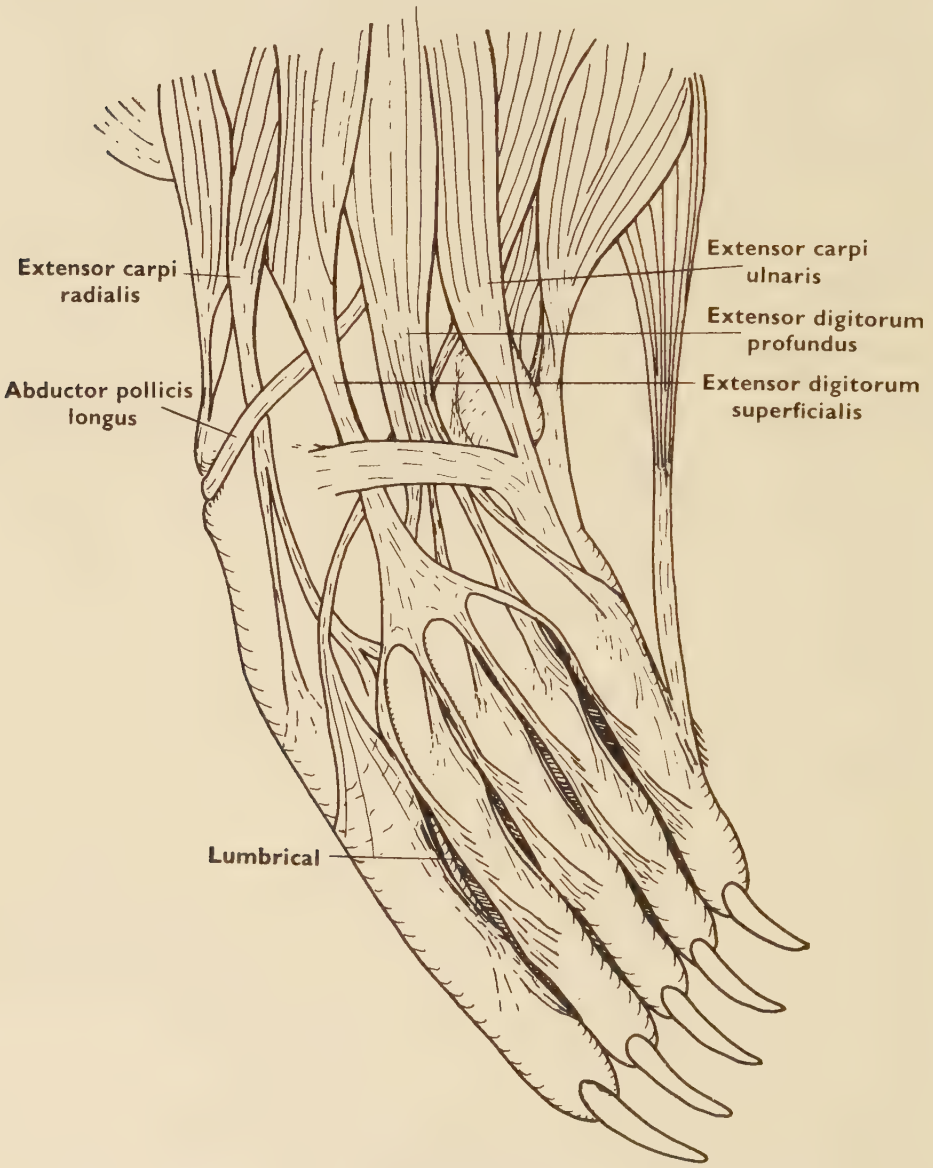

Fig. 6—Dorsal musculature of the dorsal aspect of the distal part of the grey seal forelimb.

fans out into four over the metacarpal region. These tendons approach the preaxial side of the second to fifth digits, but remain relatively free from the extensor expansion over the proximal phalanges. Each tendon then joins its respective extensor expansion on the preaxial side to be inserted into the intermediate and distal phalanges. This muscle would appear to have taken over the lumbrical function of direct interphalangeal extension in these digits (only the first digit has a lumbrical muscle).

The interosseous muscles are present in the seal but only as a single sheet arising from the ventral aspects of the metacarpals and winding round both sides of the digits to the extensor expansion of the central three digits and the central aspects of the first and fifth digits.

Abductor pollicis longus (*extensor ossis metacarpi pollicis*) is quite a large muscle arising from the lateral surface of the olecranon, the proximal half of the lateral surface of the ulna, the inter osseous membrane and the shaft of the radius. Its tendon runs onto the apex of the preaxial ridge of the radius (Fig. 6) in a well marked groove, thence in a groove on the scapholunate bone to gain an insertion into the ventro-lateral aspect of the first metacarpal bone.

The skin over the antebrachium and manus is very closely applied along the preaxial border, being bound down to the periosteum and deep fascia by heavy tough fibrous tissue. Over the postaxial aspect, however, the skin is extremely loose. In the relaxed limb this loose skin is sufficiently elastic to close up onto the flexor aspect of the limb where it lies in tight small folds. Thus when the limb is laid flat against the body wall only the smooth dorsal skin is presented to the water with the hairs running in the direction of water flow. When the limb is used as a hydroplane or a paddle, the postaxial skin is pulled out by a muscle bundle (*abductor digiti minimi longus*) arising from the olecranon to the fifth finger. By producing postaxial deviation this muscle comes to lie in the free edge of a large postaxial fold of skin which practically doubles the antroposterior width of the limb at the distal antebrachial and carpal region (Plate 1).

DISCUSSION

The inter-relationship between anatomy and observed function presents many difficulties in interpretation, largely due to accurate muscle function being little understood in any species. Even in Man, where much work has been done on a single species, in both health and disease, there is still a remarkable lack of knowledge on muscle function, and the statements on the actions of individual muscles in textbooks of human anatomy are often only partially correct, or even incorrect in a few cases. However, Man is one convenient yardstick against which function in other species can be considered. This is particularly so in the case of the seals where, in spite of detail specialization in the forelimb, there is still a reasonable comparison between the basic patterns in the two forms.

The proximal structure of the limb is short but massive, and the lack of clavicle allows wide movements of the scapula and its appendages under direct muscle control. A clavicle is commonly associated with a wide range of forelimb movements, as in the Primates, but in the case of the seals a clavicle

would limit the range of movements to some extent, particularly in a cranio-caudal direction as it does in Man. In effect the proximal muscle structure is very much in the carnivore pattern but reflecting the tremendous power required from the small limbs, not only in active propulsion, but also in the more rigid but finely controlled movements of the limb as a hydroplane. As in the Cetacea, rotation comes from the shoulder joint rather than from pronation-supination movements, which appear to be less finely controlled (and impossible in the Cetacea). The flattening of the forearm structure would in any case be valueless if pronation-supination movements were used to regulate the pitch of the hydroplane.

The massive triceps muscle extends so far down the ulna that Humphry described the *abductor digiti minimi longus* muscle as part of the triceps. However the size of this muscle is readily understood when the power of the forelimb haulage is considered, a movement in which elbow extension is extremely important, especially in the final throw forward.

The major structural and functional specializations are to be found distal to the elbow joint. By flattening the forearm the seal's limb does come to resemble that of many of the Cetacea though in the latter group the foreshortening is much more extensive proximal to the manus. The development of the preaxial prominence of the lower end of the radius is characteristic in the seal. It might be argued as did Howell that this prominence is a feature for *pronator teres* muscle, and it may well be of importance in pronation. But if the prominence were essentially a pronator ridge then the *pronator teres* should be inserted into its apex in order to gain maximum leverage, and this is not the case. The ridge is far more distalwards and in fact forms a smooth curve for the leading edge of the forelimb extending on to the manus. Along this ridge the skin and superficial tissue being heavy and tightly bound down give firmness to the curved leading edge. Running over the apex of this ridge is the *abductor pollicis longus* muscle (*extensor ossis metacarpi pollicis*), the radial deviator of the manus. In many forms, including Man, radial deviation of the manus is not a very powerful movement. This is equally true of the seal as a positive movement, but when the radial border of the limb is presented to fast moving water in ulnar deviation radial control of the manus is of major importance. It is essential therefore that the radial deviator should not only be a powerful muscle but, working as it does at a basic disadvantage, then the increased leverage obtained from crossing the apex of the radial ridge in a channel is of considerable importance.

The position of *palmaris longus* muscle superficial to the dense investing fascia is characteristic of the Pinnipedia as a whole and this is associated with the tendons of the muscle acting as a true flexor at the metacarpophalangeal joints at the same time as maintaining a superficial connection with the skin. The insertion is into the fibrous sheaths of the fingers rather than directly into the bone, but this is of minor functional importance especially since a strip runs to join the flexor sublimis tendons to the same digits. Having the preaxial sling from the distal end of the radius gives the *palmaris longus* tendons a direct flexor pull to the digits regardless of the degree of deviation of the wrist.

The *adductor digiti minimi longus* muscle is probably a morphological part of the *palmaris longus* muscle, both being superficial and from a common origin, though in its present form it is characteristic of the seal. The *palmaris longus* muscle usually has a variable part to the fifth digit which is closely linked with the abductor muscle and not slung from the radius. The Otariidae have a complicated *palmaris longus*, but no component quite like this. The otter and also the sea otter have quite a large component of *palmaris longus* going to the fifth digit in much the manner of this, but since the limb is used somewhat differently it is not of the same functional significance, nor so free.

The *abductor digiti minimi* does appear to be of remarkable value to the seal running as it does in the free postaxial border of the limb where it can bowstring the elastic postaxial material and induce and maintain considerable ulnar deviation, particularly of the fifth digit. But the muscle is not simply an abductor for it can act as a flexor at the proximal interphalangeal joint whatever the metacarpophalangeal position, and this plays an important role in the final stages of forelimb movement in terrestrial locomotion, where powerful flexion is combined with ulnar deviation (the fifth digit has no superficial flexor insertion).

The remainder of the musculature being invested in dense deep fascia is tied to the main body of the limb, but nevertheless *flexor carpi ulnaris* has a powerful sling to the preaxial border even greater in size than that of *palmaris longus*. This sling is not however particularly important for the true *flexor carpi ulnaris* component running to the pisiform bone but is linked with the large specialized portion of the muscle which crosses to the preaxial border of the limb and goes thence to the proximal phalanges. Without the sling this component would tend to displace the main flexor mass of tendons which run beneath it, but, slung as it is, the combined parts of *flexor carpi ulnaris* act as the superficial part of a carpal tunnel. The most remarkable feature of this muscle in the seal however is its heavy tendons which run to the proximal phalanges of all the digits. The animal is thus equipped with not only the usual flexores of the metacarpophalangeal joints, the *interossii*, albeit somewhat small, but also extremely powerful long flexors in the *flexor carpi ulnaris* to all digits and *palmaris longus* to the second to fifth digits. In addition *flexor carpi ulnaris* retains its normal flexor-ulnar deviating function.

Metacarpophalangeal flexion is a major muscular problem in the seal for it must be able to operate an efficient system of digital flexion both with metacarpophalangeal flexion or hyper-extension, and this hyper-extension may be as much as 60°. In many animals the *interossii* are important flexors of the metacarpophalangeal joints, as in Man, but their position is so deep and, as in Man, the tendons run dorsal to the transverse palmar ligament that in metacarpophalangeal hyper-extension they cease to be effective flexors and they can even become converted into extensors in marked hyper-extension. Hence in the majority of carnivores—and especially the seals—their function as flexors will be limited and so another and due to the range of movement involved, a long flexor is required. This role is carried out in many canivora—e.g. the otters by *palmaris longus*, a role maintained in the seals but amplified by a specialized and extremely powerful *flexor carpi ulnaris* which will operate

particularly with ulnar deviation. This latter muscle is of particular importance in terrestrial locomotion in which the ulnar flick is used together with flexion.

The smallness of the *flexor digitorum sublimis* muscle is readily understood when it is considered that the main grip in the seal manus comes by flexion at the terminal interphalangeal joints. If the proximal interphalangeal joints were concurrently flexed to the same degree as the distal, then the terminal phalanx would lose its power to flex quite so readily onto the more proximal part of the digit and thus the grip would be less efficient. With the present arrangement the terminal phalanx can close almost like a jack knife blade onto the proximal part of the digits.

The double extensor muscular system is of course not a characteristic feature of the seal though few animals have a complete double set to all four postaxial digits. But the insertions of these muscles is in a way which is uncommon. The deeper extensor muscle forms the basis of the extensor expansion and is also inserted into the proximal phalanx. This muscle compares very closely with *extensor digitorum communis* of Man. In Man the long extensor acts primarily as an extensor at the metacarpophalangeal joint. Unless hyper-extension is prevented at this joint the interphalangeal joints are not extended and the finger takes up a position rather like a mild version of the haulage grip of the seal. Simple flexion from this position at the metacarpophalangeal joints either by the *interossii* or by an external force will produce a spontaneous extension of the interphalangeal joints. Alternatively the lumbricals are direct interphalangeal extensors but they are fairly weak muscles. Interphalangeal extension is thus rather a weak movement in Man and is not of prime functional importance. In the seal however, the digits are used powerfully in both metacarpophalangeal hyper-extension with interphalangeal flexion and also in full metacarpophalangeal and interphalangeal extension. The system found in Man would not be satisfactory for this double function. The seal however has the deeper extensor muscle arranged in a way suitable to operate upon the metacarpophalangeal joints in consort with the *extensor pollicis longus* of the first digit. In addition the superficial flexor runs directly to the extensor expansion over the interphalangeal joints, replacing the lumbrical muscle to the postaxial four digits. The first digit with its single interphalangeal joint has a true lumbrical muscle but no superficial extensor.

SUMMARY

The patterns of locomotion observed in certain species of seals have been described both on shore and in the water. Some species, e.g. the grey seal (*Halichoerus grypus*) make use of the forelimb for a wide range of activities, a range quite remarkable among vertebrates. Those movements are described together with certain features of forelimb anatomy which are considered to be of especial note. The functional significance of morphological features of the phocid forelimb are discussed in the light of the locomotor activities described.

Fig. A.—Dorsal view of the forelimb of an elephant seal. White headed pins have been inserted to show the ulnar border of the limb with the postaxial fold of skin stretching from 5th digit to the body wall.

Fig. B.—Ventral view of forelimb of an elephant seal showing the thickness of abductor digiti minimi muscle in the postaxial skin border. Note also the firm dense nature of skin (turned back) and subcutaneous tissue over the radius compared with the postaxial skin.

Photograph of a grey seal pup illustrating digital haulage grip in the forelimbs.

Fig. A.—Dorsal view of the carpal region of a grey seal articulated forelimb.

Fig. B.—Wrist joint of forelimb of plate 4 opened in flexion, i.e. volar aspect contiguous to show the surface features of the scapho-lunate bone above and radius below.

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Figures 2 and 3 were drawn by Miss Dorothy Mustart, and photographs of Plates 1 and 3 by Mr K. W. Iles.

REFERENCES

Backhouse, K. M. (1954). The grey seal. *Univ. Durh. Med. Gaz.* **48** : 9–16.

Duvernoy, G. L. (1822). Recherches anatomique sur les organes du movement du phoque commun, *Phoca vitulina*, L. *Mem. Mus. Hist. nat., Paris* **9** : 49–70, 165–189.

Howell, A. B. (1929). Contribution to the comparative anatomy of the eared and earless seals (genera *Zalophus* and *Phoca*). *Proc. U.S. nat. Mus.* **73** : Art. 15.

Howell, A. B. (1930). *Aquatic mammals.* Baltimore.

Humphry, G. M. (1868). On the myology of *Phoca communis*. *J. Anat., Lond.* **2** : 290–322.

Lucae, J. C. G. (1887). Die Robbe und die Otter in ihrem Knocken und Muskelskelet. *Abh. senckenb. naturf. Ges.* **8** : 277–378.

Matthews, L. H. (1952). *British mammals.* London.

Miller, W. C. S. (1887). The myology of the Pinnipedia. *Challenger Rep.* **26** Pt. 67 : 139–234.

GENERAL DISCUSSION

Chairman : Professor Sir James Gray, C.B.E., F.R.S.

Mr O'Gorman : Dr Backhouse is describing what is normally regarded as the phocid type of locomotion. Two or three of the Antarctic species of phocids spend more time on the ice than on land in summer and show movement by a lateral swing of the pelvis. The Crab-eater and Leopard seals can travel at considerable speeds, the former up to 12 m.p.h. by this means. Both types of movement, the lolloping and lateral pelvic movement have been seen in Crab-eaters at quite slow " walking " speeds.

LOCOMOTION AND LOCOMOTORY ORGANS IN WHALES AND DOLPHINS (CETACEA)

BY

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Zoological Laboratory, University of Amsterdam

This paper is a review of the present status of our knowledge of the locomotion and the locomotory organs in whales and dolphins. Experiments on the dorso-ventral flexibility of the body of the Common Porpoise have shown that the thorax and the lumbar region are very rigid, but that there are regions of very great mobility at the base of the tail (anal region) and at the junction of the peduncle of the tail and the tail-fin (flukes). Films of swimming Bottle-nosed Dolphins and a Pigmy Sperm Whale show the same centres of mobility during locomotion under water. The movements of the tail are exclusively up and down, the tail-fin makes an angle with the peduncle of the tail in such way that it can exert a forward driving force on the water. The peduncle of the tail meets but little resistance.

Cruising speed and maximum speed appear to be almost the same in the small dolphins and in the big whales. This phenomenon can be explained by assuming that the flow of the water along the body of the dolphin is wholly laminar, but that in the big whales it is partly laminar and partly turbulent. The difference may be connected with the absolute size of the animals or with their shape, but it is also possible that the efficiency of the spinal muscles plays an important part in determining the speed of the animals.

The efficiency of the spinal muscles probably depends to some extent on the position of the mammillary processes in the posterior lumbar and the anterior caudal region. In the big whalebone whales the position of these processes is close to the vertebral bodies, but in porpoises and dolphins they are shifted upward. Consequently the force exerted by the muscle fibres and tendons of the longissimus and transversospinalis muscles, inserted into the mammillary processes in the regions mentioned, is increased because it is transmitted to the vertebral bodies by a very long lever arm.

The structure of the vertebral column and the spinal musculature is described. In the three divisions of the epaxial musculature as well as in the hypaxial musculature the components of the different regions are fused into single muscular masses ranging from the occiput to the tip of the tail, although the different components still may be distinguished by their innervation. The presence of long muscle fibres enables the tail to make large excursions. The development of the muscles and the insertion of the tendons is adapted to the mobility of the body-axis and especially to the centres of mobility in the anal region and at the base of the flukes. This is especially apparent in dolphins.

CONTENTS

	Page
General remarks—mobility	77
Locomotion	79
Locomotory organs	84
Summary	92
References	93
General discussion	94

GENERAL REMARKS—MOBILITY

Whales and dolphins are exclusively aquatic mammals with a streamlined, torpedo-shaped body. From species to species this shape may show a certain

variation. Some are very slender (dolphins, ziphiids, rorquals), some are rather clumsy (Right whales, Sperm whale). The species may differ moreover with regard to the relative length of the tail and the position of the flippers (pectoral fins) (Fig. 1) or with regard to the presence or absence of a dorsal fin.

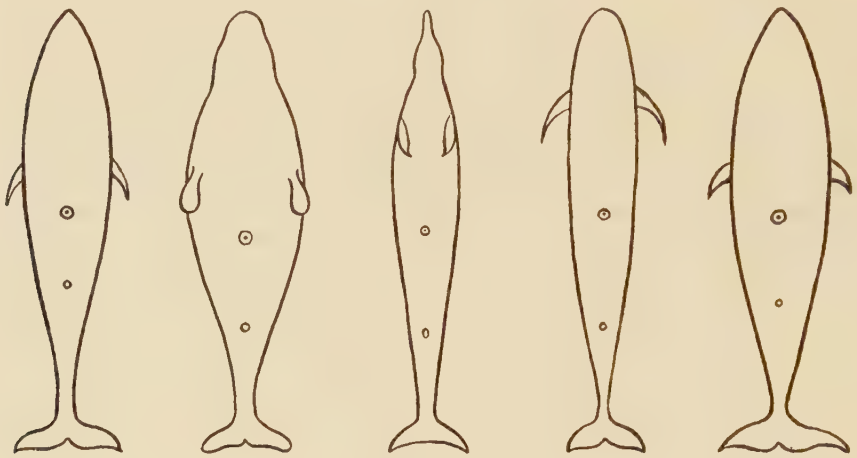

Fig. 1—Body-shape of five different whales and dolphins. The umbilicus and the anal aperture are indicated. From left to right : Sei Whale (*Balaenoptera borealis* (Lesson)), Sperm Whale (*Physeter macrocephalus* L.), Sowerby's Whale (*Mesoplodon bidens* (Sowerby)), Pilot Whale (*Globicephala melaena* (Traill)), Common Porpoise (*Phocaena phocaena* (L.)). All animals are reduced to the same length. From Slijper, 1958.

Generally, fast swimmers like rorquals and dolphins have a slender body with a dorsal fin. In slow swimmers the shape of the body is usually clumsier and the dorsal fin may be absent. All species lack external hind limbs ; the internal parts are only represented by a rod-like, rudimentary pelvic bone, that is not attached to the vertebral column.

The part of the body behind the anal aperture is called the tail. It narrows gradually towards its posterior end where it broadens abruptly into the horizontally expanded tail-fin. In the central part of this fin the vertebral column is represented by a series of small dorso-ventrally compressed caudal vertebrae, but the lateral parts of the fin (the flukes) consist only of a very tough subepidermal connective tissue. The fibres of this tissue are connected with those tendons of the spinal musculature that are attached to the vertebrae of the tail-fin (Roux 1883). The flukes are expanded in the horizontal plane because whales and dolphins are mammals. Contrary to fishes and reptiles, whose principal body movements are in the horizontal plane (laterally), the principal body movements of the mammals are in the vertical plane as may be seen in a galloping dog or cat. Consequently the body-axis of the Cetacea is also moved mainly in the vertical plane (up and down), and the flukes must be horizontal instead of vertical as in fishes and reptiles.

In terrestrial mammals the centre of motion of the body-axis is situated in the region of the so-called diaphragmatic or anticlinal vertebra, that is

usually found in the posterior thoracic region.* It is mostly represented by one of the last thoracic vertebrae (see Slijper 1946). In ungulates the centre of motion lies in the lumbo-sacral joint. Experiments on the dorso-ventral flexibility of the body of the Common Porpoise (*Phocaena phocaena* (L.))

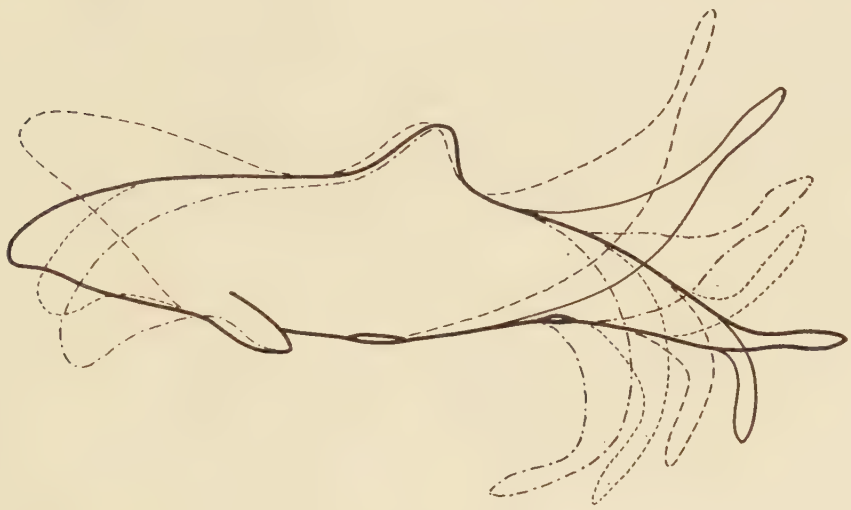

Fig. 2—Flexibility of the body of a Common Porpoise (*Phocaena phocaena* (L.)) in the vertical plane. From Slijper, 1936.

(Fig. 2) show that in this respect the Cetacea differ markedly from their terrestrial relatives (Slijper 1936, 1946). The short cervical region has a certain degree of mobility, but the thorax and the anterior part of the lumbar region are rigid and show only a very small degree of mobility. The posterior lumbar region is a little more mobile and a point of extreme mobility is situated in the anal region, i.e. at the base of the tail. The tail itself is fairly mobile. At the junction of the tail and the tail-fin (the flukes) there is a second centre of extreme mobility. The flukes themselves are fairly rigid.

LOCOMOTION

Underwater films have been made of the swimming movements of dolphins and sperm whales. Those made in the Marineland Aquarium (Florida) show particularly well that the swimming movements of the Bottle-nosed Dolphin (*Tursiops truncatus* (Mont.)) and the Pigmy Sperm Whale (*Kogia breviceps* (Blainv.)) fully correspond with the mobility of the body and tail of the Common Porpoise. The anterior part of the body shows almost no movements required for ordinary locomotion, although from time to time the animals

* The diaphragmatic vertebra is the vertebra in which the position of the articular surfaces of the zygapophyses (articular processes) changes from the horizontal into the vertical position. The anticlinal vertebra is the vertebra in which the neural spine changes its direction. In the pre-anticlinal vertebrae it is inclined caudally, in the post-anticlinal vertebrae it is inclined cranially. In many species the diaphragmatic vertebra is the same as the anticlinal vertebra. In the other animals they are near each other (Slijper, 1946).

make movements of the head, that may be necessary for orientation or for catching prey. A special centre of extreme mobility is situated at the base of the tail (anal region) and another one at the junction of the peduncle of the tail and the flukes. The movements of the tail are exclusively up and down. There are no indications of a sculling movement as has sometimes been described in the literature.

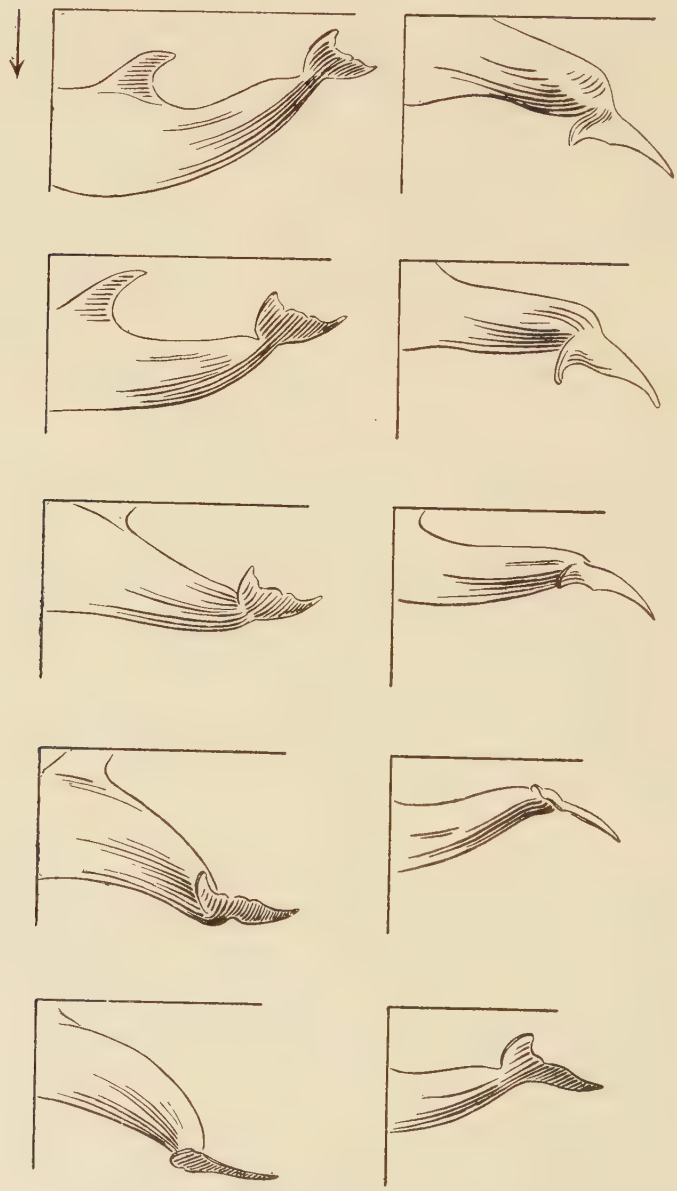

Fig. 3—Ten stages of the motion of the tail and flukes taken from a film of a swimming Bottle-nosed Dolphin (*Tursiops truncatus* (Mont.)) in the Aquarium Marineland, Florida. Modified after Parry, 1949, from Slijper, 1958.

Parry (1949) has made an analysis of these movements. It shows that in the upstroke as well as in the downstroke the flukes make an angle with the peduncle of the tail (Fig. 3). It gives the impression that during the up and down movements the flukes remain a little bit behind, which means that during the downstroke they exert on the water a force in a ventro-caudal direction, whereas during the upstroke they exert a force in a dorso-caudal direction. The dorsal and ventral components of these forces neutralize each other and the resultant force in the caudal direction drives the animal forward through the water (Fig. 4). It is very difficult to determine whether the

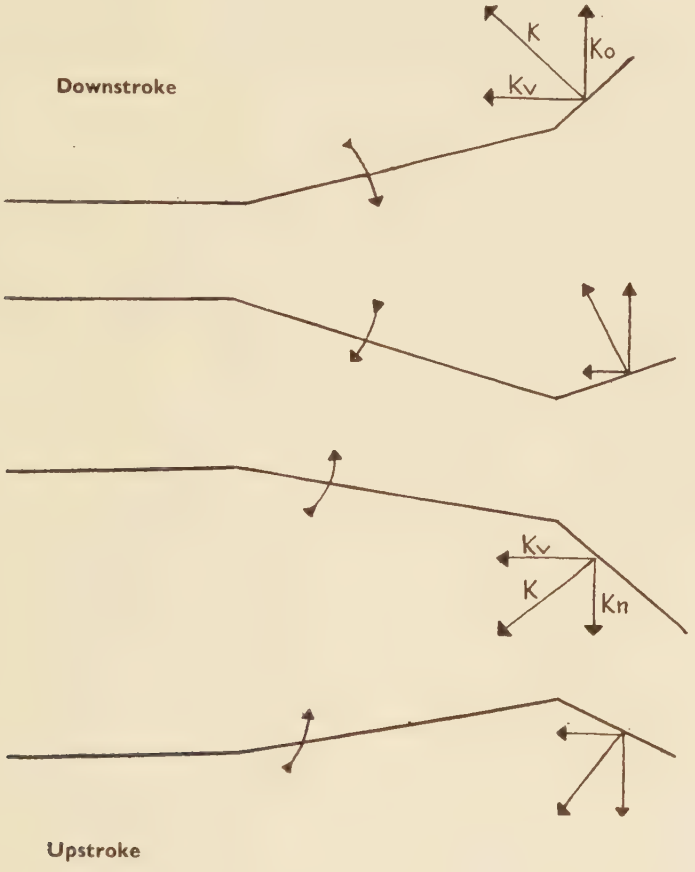

Fig. 4—Forces exerted on the water during the upstroke and downstroke of the tail of a swimming dolphin. From Slijper, 1958.

movements of the flukes against the peduncle of the tail are passively caused by the resistance of the water or whether they are actively effected by contractions of the muscles of the tail. The fact, however, that a special bundle of tendons of the tail muscles runs to the vertebrae of the tail-fin, may serve as an indication that the position of the flukes in relation to the peduncle of the tail is caused, or at least controlled, by contractions of this special part of the musculature.

In its up- and downward movements, the peduncle of the tail meets only very little resistance in the water. One might say this part of the tail cuts the water like a knife because it is laterally compressed and tapers off rather sharply at the upper and lower side. A cross section through the tail shows that this particular shape is caused by high crests of subcutaneous blubber at both the upper and lower side of the tail (Fig. 5).

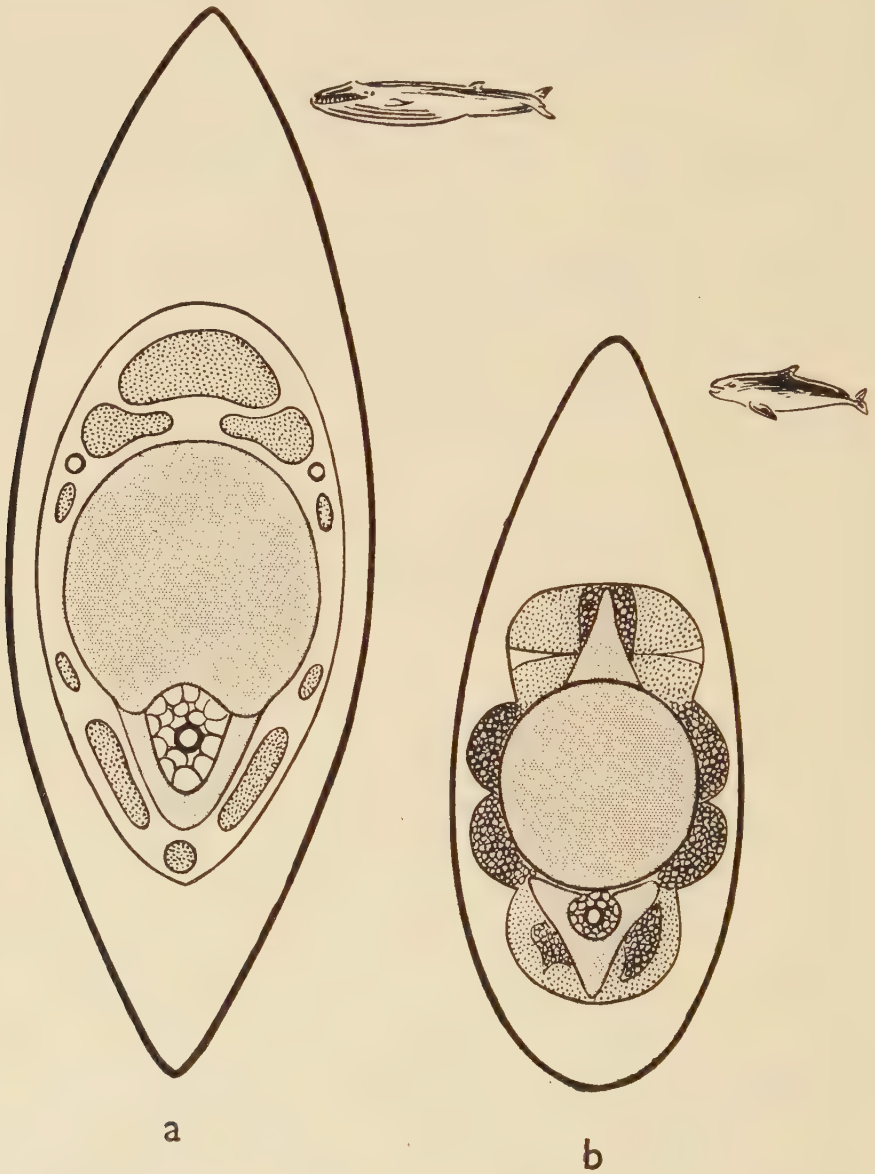

Fig. 5—Cross section through the peduncle of the tail of a Blue Whale (*Balaenoptera musculus* (L.)) (left) and a Common Porpoise (*Phocaena phocaena* (L.)) (right).

The movements described above are seen when the animals swim in a straight line. When they make a turn, lateral movements of the head and tail as well as different movements of the flippers and flukes may be observed. Experiments have shown that the body of the Common Porpoise shows the same mobility and rigidity with regard to the mobility in the horizontal plane (lateral movements) as have been described with regard to the movements in the vertical plane, with this exception, however, that at the base of the flukes there is no special centre of great lateral mobility (Slijper, 1936).

Woodcock (1948) observed that in dolphins swimming at a speed of 20 m.p.h. the tail moved with a frequency of two strokes up and down per second. This is confirmed by Gunther (1949), who recorded 1–2 strokes per second in a Fin Whale (*Balaenoptera physalus* (L.)) swimming at a speed of 10–12 knots.

It is not easy to say what is the swimming speed of whales and dolphins. In the first place there are very great differences between the different species and in the second place a distinction must be made between animals swimming in a sprint at a speed they can maintain only during a few minutes, and those swimming at cruising speed, which they can maintain for hours. A third type of locomotion that is called riding on the bow wave of a ship, is often observed in dolphins. In this case the body of the animal seems to be motionless. The details of this way of swimming are not yet fully known, but it appears to be related to the so-called " surf-riding " of man. Probably the flukes are brought in such position that the animal is propelled by the up-welling water of the bow wave. It has been studied—among others—by Hayes (1953), Woodcock & McBride (1951) and by Scholander (1960).

Right Whales (Balaenidae), Grey Whales (*Eschrichtius gibbosus* (Erxleb.)) and Humpbacks (*Megaptera nodosa* (Bonnat.)) appear to be slow swimmers, their cruising speed being about three knots and their top speed about seven knots. Sperm Whales (*Physeter macrocephalus* L.) may show short sprints of 16–20 m.p.h., but their normal speed in most cases does not exceed six miles an hour. Recent observations of Fin Whales (*Balaenoptera physalus* (L.)), that were frightened by the Asdic apparatus of whale catchers, have shown that they could leave the range of this apparatus within a few seconds, demonstrating thereby that they can reach a speed of 30–40 m.p.h. This speed was already known for the Sei Whale (*Balaenoptera borealis* Lesson)) (see Andrews 1914) and it may be supposed that the Blue Whale (*Balaenoptera musculus* (L.)) may also attain this speed. The normal cruising speed of these rorquals as well as of the Minke Whale (*Balaenoptera acutorostrata* (Lacép.)) is 10–15 miles.

Almost the same speed has been observed in dolphins. Several observers (among others Captain Mörzer Bruins ; see also Lane 1953 and Gunter 1943) have stated that Common Dolphins (*Delphinus delphis* L.), Bottle-nosed Dolphins (*Tursiops truncatus* (Mont.)), Red Sea Bottle-nosed Dolphins (*Tursiops aduncus* Ehrenberg), False Killers (*Pseudorca crassidens* (Owen)) and some species belonging to the genera *Prodelphinus* and *Steno* can maintain a speed of 15–20 m.p.h. during a fairly long time, even when they do not swim on the bow wave of a ship. According to Backhouse (1960) a sprint of 25 knots has been observed in the Common Dolphin. Freshwater dolphins appear to

be slower. Layne (1958) observed a cruising speed of two miles and a top speed of ten miles in the Boto (*Inia geoffrensis* Blainv.), whereas six miles has been observed in a dolphin of the Indian coastal waters (*Sotalia plumbea* Cuv.).

All these data clearly show that in any case whales and dolphins are able to attain an underwater speed that is much higher than that of an ordinary submarine (six to eight miles). Another very remarkable phenomenon is the fact that on the average the speed of the small dolphins is the same as that of the big whales whose weight is about 1000 times that of their small relatives. In ships of the same type the speed generally increases with the size of the ship. The explanation of the phenomenon was discussed at length at the annual meeting of the British Association for the Advancement of Science in 1949. Especially by the work of Gray (1936 ; see also Gray & Parry 1948), Kermack (1948) and Hill (1950) it has been shown that the phenomenon might be explained by assuming that the flow of the water along the body of the dolphins is entirely laminar, but that along the body of the big whales it is partly laminar and partly turbulent. It may be supposed, for example, that along the anterior two thirds of the body it is laminar, whereas it is turbulent among the posterior one third. A turbulent flow causes a much higher resistance and consequently a much lower speed than a laminar flow.

It cannot yet be proved that along the body of a dolphin there is indeed an entirely laminar flow of the water, because it has not yet been possible to make experiments with a model that shows the same active motions as the body of a swimming animal. It may be assumed, however, that along such a body the flow differs from that along a rigid or along an only passively movable model. Probably it is entirely laminar. Observations made by Steven (1950) of dolphins swimming in a phosphorescing sea, give a strong indication that an entirely laminar flow indeed occurs. If this is true, it may be further assumed that the difference between the dolphins and the whales is in the first place connected with the length of the body because the longer the body is, the sooner a turbulent flow will arise. In the second place it may also be connected with the shape of the body. The further the greatest girth of the body lies to the anterior, the greater is the possibility that the flow will be turbulent. The greatest girth of the body is found more to the anterior in whales than in dolphins. In the United States of America some people engaged in technical research hold the opinion that the laminar flow may be connected with the way in which the epidermis of Cetacea is attached to the underlying layer of blubber, viz. : by means of very long papillae. With the aid of a silica-gel some models have been constructed, but definite results are not yet available.

LOCOMOTORY ORGANS

The principal locomotory organ of whales and dolphins is the body-axis, i.e. the vertebral column and the spinal muscles of the back and tail. The flippers (pectoral fins) are only used in very slow motion and in steering, but the abdominal musculature and the *levator ani* muscle may assist the muscles on the ventral side of the vertebral column (hypaxial muscles) to a certain degree. The neck is very short (Fig. 6) and has always seven cervical vertebrae. These are highly compressed in the longitudinal direction, and in Right whales,

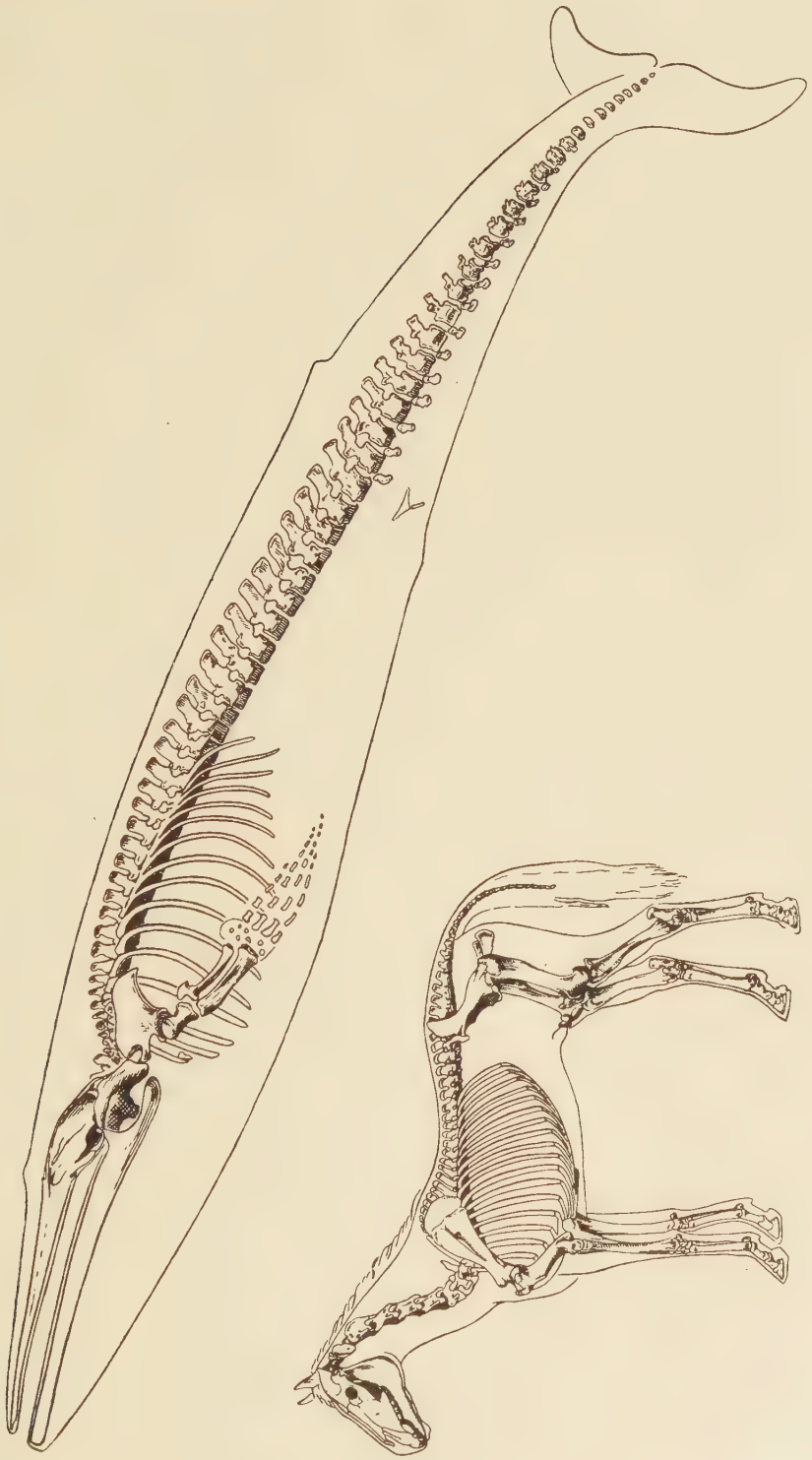

Fig. 6—Comparison of the skeleton of a Blue Whale (*Balaenoptera musculus* (L.)) and a horse. From Slijper, 1958.

dolphins and porpoises they are fully or partly coalesced. Consequently the mobility of the head mainly depends on the occipital joint, which in some dolphins is fairly mobile but which may be restricted in its motion in others, as for instance in the Pilot Whale (*Globicephala melaena* (Traill)). The shortness of the neck and its rigidity are necessary because the propulsive powers of the animal are concentrated in the posterior part of the body-axis.

The number of thoracic vertebrae is almost the same as in terrestrial mammals. They show a very small degree of mobility. The lumbar region is very much lengthened, sometimes by an increase of the number of lumbar vertebrae, sometimes by an increase in length of the vertebral bodies and sometimes by a combination of both phenomena. The same may be observed in the tail. The highest total number of vertebrae is found in the White-beaked Dolphin (*Lagenorhynchus albirostris* Gray) which has 93 vertebrae, but even a Blue Whale with 63 has more vertebrae than a dog, which has 50. A distinct tendency to increase in the number of vertebrae is also apparent when the geologically younger representatives of the different groups of Cetacea are compared with their older relatives. This increase in number of the vertebrae causes an increase in mobility and elasticity of the vertebral column because the amount of cartilage (intervertebral discs) is greatly increased, especially when the vertebral bodies are comparatively thin (short) as for example in dolphins.

There is no sacrum because the rudimentary pelvic bone is not attached to the vertebral column, but the original sacral vertebrae can still be found by determining the nervous roots that are homologous with those leaving the vertebral canal between the sacral vertebrae in terrestrial mammals (plexus pudendus). If the sacral vertebrae are determined in this way, it appears that the first caudal vertebra does not follow immediately on the last sacral. In the Common Porpoise (*Phocaena phocaena* (L.)), for example, there are six so-called postsacral vertebrae.

The first caudal vertebra lies at the level of the anal aperture. All caudal vertebrae—with the exception of those of the flukes—bear at the ventrocranial side of their bodies a pair of chevron bones (Fig. 6). As with the very long neural spines at the dorsal side of the lumbar and caudal vertebrae and the long transverse processes at their lateral side, so these chevron bones at the ventral side give the muscles a large surface for their origin and a long lever arm for their inserting tendons. The principal task of the body-axis in whales and dolphins is not to carry the body-weight, as in terrestrial mammals, but to serve as a surface for the attachment of the locomotory muscles.

The musculature of the Cetacea is very well developed. In the big Blue Whale (*Balaenoptera musculus* (L.)) the total weight of the musculature is about 40 tons, i.e. 40 per cent of the body weight (weight of the skeleton 17 per cent), and in some other whales and dolphins it may be even about 50 per cent. The musculature is characterized by the fact that the muscles of the neck, the trunk and the tail are completely fused. Consequently each of the three big epaxial muscular systems is represented by one single functional unit ranging from the occiput to the tip of the tail. Apart from the muscles at the ventral side of the cervical vertebrae, the hypaxial muscula-

ture consists also of a practically indivisible muscular mass, ranging from the last four or five ribs to the tip of the tail. It originated from the fusion of the psoas-muscles (which are not attached to the rudimentary pelvic bone) with the musculature of the ventral side of the tail. The components may still be distinguished by their innervation, and this innervation also shows that the original border between the muscles of the trunk and those of the tail (epaxial and hypaxial) lies at the level of the anal aperture and the first chevron bone. All these muscular systems show a distinct tendency to develop long muscular and tendinous fibres, but a certain number of short fibres can still be distinguished. The presence of long muscular fibres means that, especially in the tail, large excursions can be made.

In the toothed whales the *iliocostalis* muscle expands as a broad sheet over the lateral surface of the ribs, but in whalebone whales the thoracic part is comparatively narrow. The lumbar part, continued in the tail as the *intertransversarii caudae dorsalis et ventralis*, is a comparatively narrow muscular band embracing the outer part of the transverse processes. This muscle is not very strongly developed but its effect is highly enlarged by the lever-arm of the long transverse processes. A part of the lumbo-dorsal fascia separates the *iliocostalis* from the adjacent spinal muscles, but a fascial separation between the *longissimus* and the *transverso-spinalis* is only present in the tail.

In terrestrial mammals the majority of the fibres of the *longissimus dorsi* show an arrangement around the diaphragmatic (or anticlinal) vertebrae (Fig. 7 ; Slijper 1946). Most of the fibres originate from the pre-diaphragmatic vertebrae and their ribs ; they are inserted into the neural spines and the mammillary processes of the postdiaphragmatic vertebrae. In ungulates there are strong sacral attachments. Because of the different type of mobility of the vertebral column in Cetacea, the *longissimus* complex of these animals originates at the occiput, at the ribs and at the transverse processes and neural arches of all thoracic, lumbar and caudal vertebrae as far back as the middle of the tail. There are three systems of inserting tendons, viz. (Figs. 8 and 9) : 1. Superficial tendons running to the summits of the neural spines from the first lumbar vertebra to the vertebra that lies at the junction of the peduncle of the tail and the flukes. 2. Deep tendons running to the mammillary processes from the first thoracic vertebrae to the junction of the tail fin and the peduncle of the tail. 3. A special system of long tendons inserted into the vertebrae of the flukes.

In terrestrial mammals the fibres of the *transverso-spinalis* show the same arrangement around the diaphragmatic vertebra as those of the *longissimus*. The fibres of the *semispinalis* and *spinalis* originate at the neural spines of the prediaphragmatic vertebrae. They are inserted into the mammillary processes and the neural spines respectively of the postdiaphragmatic vertebrae (Fig. 7). In all Cetacea there is an undifferentiated *transverso-spinalis*, reaching from the skull or the first cervical vertebrae to the junction of the tail and the flukes. In the neck and thorax it consists almost entirely of *multifidus*- and shorter fascicles, but in the caudal part of the thorax the number of *semispinalis* fibres increases and in the lumbar and caudal region there may be even very long muscular fascicles and tendons. All tendons are inserted into the mammillary

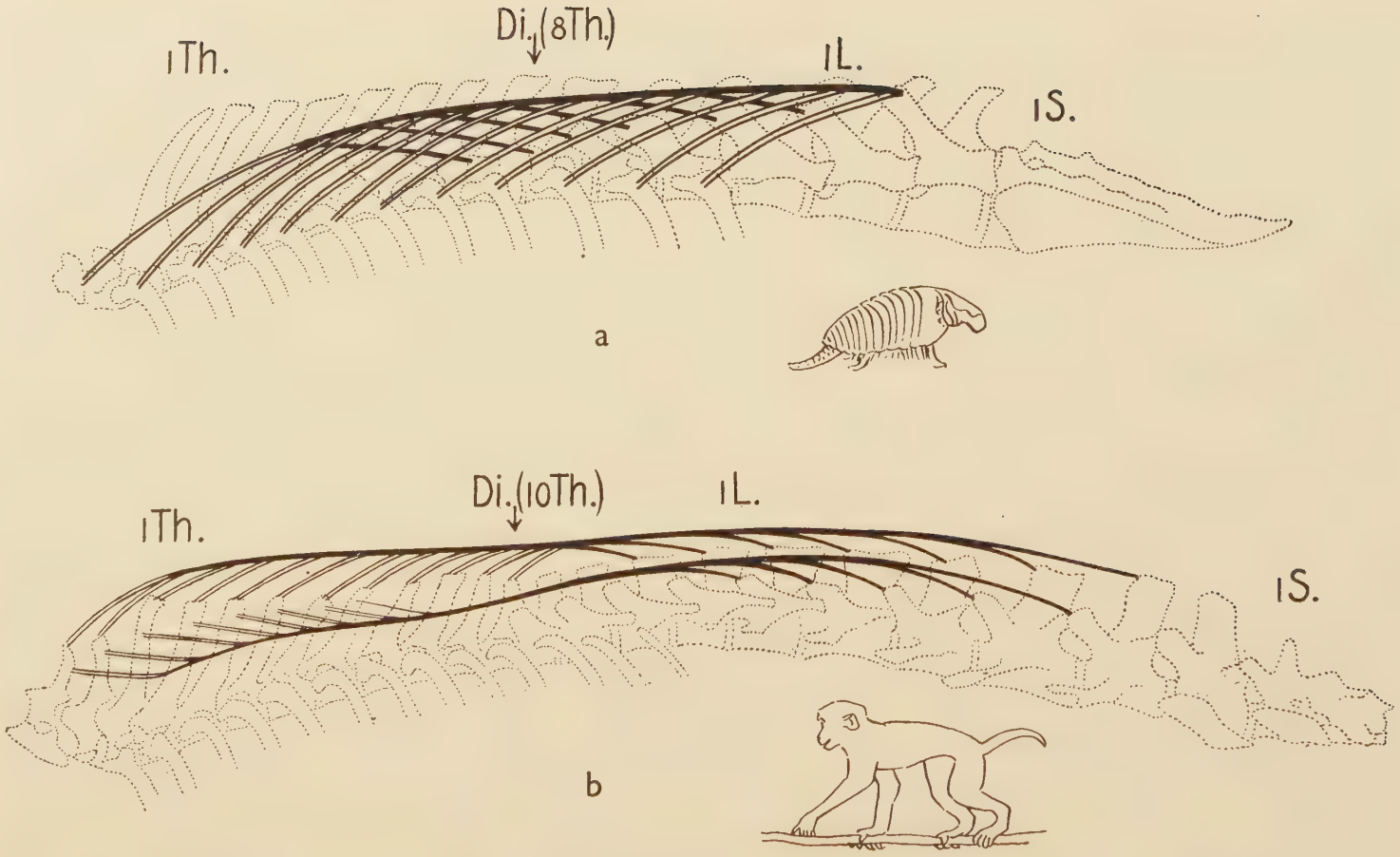

Fig. 7—Above : Schematic drawing of the structure of the *longissimus dorsi* muscle in the Peba-Armadillo (*Dasypus novemcinctus* L.). Below : Schematic drawing of the structure of the *transverso-spinalis* muscle in the Macaque (*Nemestrinus nemestrinus* (L.)). From Slijper, 1946.

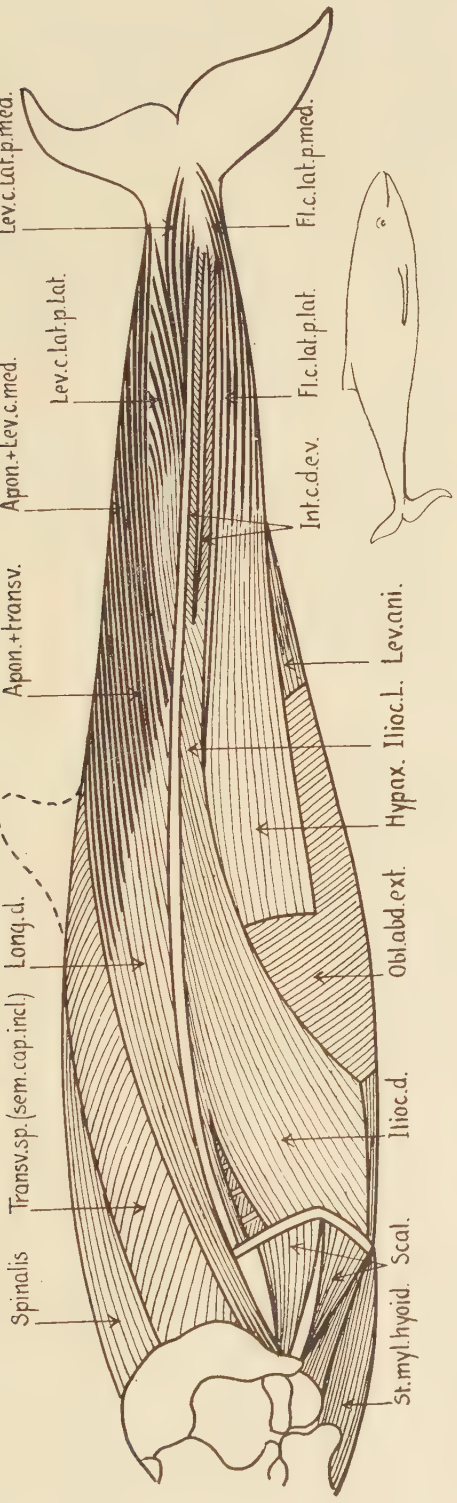

Fig. 8—Musculature of the trunk and tail of the Common Porpoise (*Phocaena phocaena* (L.)). *Apon.* = superficial tendons of *m. longissimus dorsi*. *Lev. c. lat.* = tendons of *longissimus* complex inserted into mammillary processes. *Lev. c. lat. p. med.* = tendons of *longissimus* complex inserted into the vertebrae of the flukes.

processes (Fig. 9). There are no *spinalis* fibres and there is not the slightest relation to a diaphragmatic vertebra.

From the functional point of view the arrangement of the muscular fascicles and tendons of the hypaxial muscles is almost the same as in the epaxial musculature. There are tendons running to the tip of the chevron bones, tendons inserted into the lateral surface of the chevrons and special tendons running to the vertebrae of the flukes.

Fig. 9—Schematic drawing of the insertion of the tendons of the *longissimus* complex and the *transverso-spinalis* into the neural spines and mammillary processes of the posterior lumbar vertebrae in a baleen whale.

Because the muscular bundles are not arranged around a diaphragmatic vertebra nor around any other special vertebra, there is no anticliny of the neural spines, as can be observed in a great number of terrestrial mammals. In Archaeocetes, baleen whales (Mystacoceti) and beaked whales (Ziphiidae) the presence of a centre of mobility at the base of the tail has no influence on the structure of the musculature or on that of the vertebral column. In these animals all mammillary processes are situated at the same, comparatively short, distance from the vertebral bodies. All neural arches have almost the same length and are comparatively short. All neural spines are inclined backward and make about the same angle with the vertebral bodies (Fig. 10).

In sperm whales (Physeteridae), River dolphins (Platanistidae), dolphins (Delphinidae) and porpoises (Phocaenidae) the presence of a well-marked centre of mobility in the anal region has exerted a very distinct influence on the structure of the vertebral column and the spinal musculature. Some species show only a shifting upward of the mammillary processes in the posterior lumbar and anterior caudal region (*Physeter*, *Pseudorca*, *Inia*, *Stenodelphis*), others show a shifting upward of the mammillary processes combined with an anticliny of the neural arches : the neural arches of the posterior lumbar and anterior caudal vertebrae being inclined in the cranial direction, whereas the other neural arches stand upright or are inclined caudally (*Delphinapterus*,

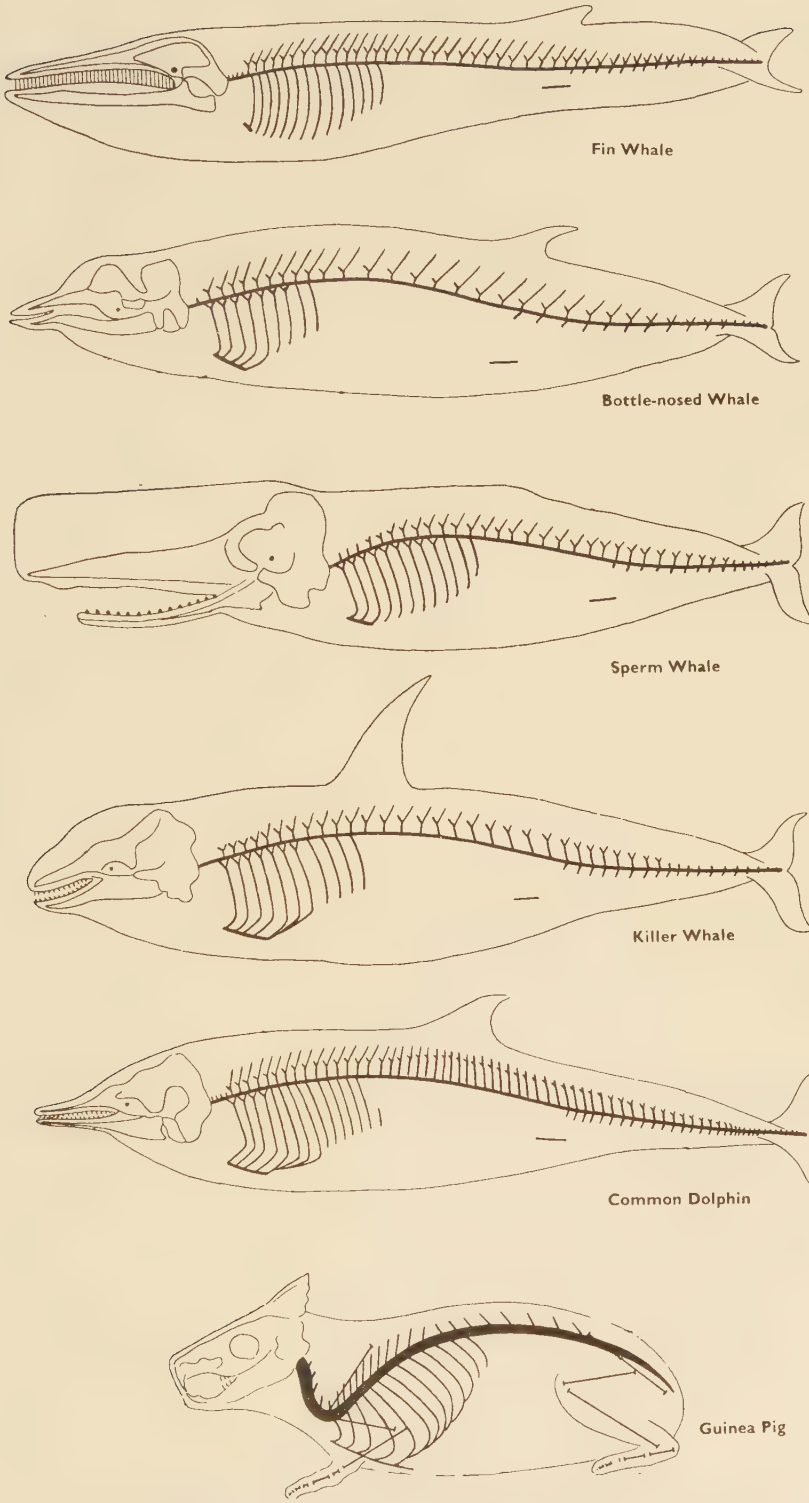

Fig. 10—Schematic drawing of the skeleton of five Cetacea, to show the different types with regard to the position of the mammillary processes and the direction of the neural arches and neural spines. Fin Whale (*Balaenoptera physalus* (L.)), Bottle-nosed Whale (*Hyperoodon ampullatus* (Forster)), Sperm Whale (*Physeter macrocephalus* L.), Killer (*Orca orca* (L.)), Common Dolphin (*Delphinus delphis* L.). Below : Guinea Pig, a typical terrestrial mammal. From Slijper, 1958.

Orca, *Kogia*, *Lipotes*). More specialized species show a very great shifting upward of the mammillary processes combined with a forward inclination of the neural arches as well as the neural spines in the posterior lumbar and the anterior caudal region (*Platanista*, *Phocaena*). In these animals the neural arches are very long, the neural spines comparatively short. Representatives of the genera *Delphinus*, *Prodelphinus*, *Lagenorhynchus* and *Grampus*, show the same phenomenon along with a very significant reduction in size of the mammillary processes in the middle and posterior part of the lumbar region. In this region these processes may even be completely absent. In the tail they suddenly reappear and here they are very well developed.

The shifting upward of the mammillary processes gives a longer lever arm to the inserting tendons of the *longissimus* and the *transverso-spinalis* in the posterior lumbar and the anterior caudal region. This phenomenon is certainly connected with the high mobility of the anal region, as is particularly noteworthy in those species where the mammillary processes of the middle and posterior lumbar region are poorly developed or even lacking. The tendons inserted into these processes are apparently also poorly developed because the anterior caudal region is moved against a comparatively rigid lumbar region. The shifting upward of the mammillary processes also causes an enlargement of the area of origin at the neural arches of those fibres of the *longissimus* that are inserted into the vertebrae of the flukes and are supposed to originate in the posterior lumbar and anterior caudal region.

The cranial inclination of the neural arches and even (in some species) of the neural spines may be connected with the prevalence of the *longissimus* in the muscular systems that are inserted into these vertebrae. It has been demonstrated that vertebral processes show a tendency to attain a direction perpendicular to that of the muscles or tendons attached to them (Slijper 1946). The prevalence of the tendons of the *longissimus* attached to the mammillary processes and the summits of the neural spines of the vertebrae involved, may have caused their forward inclination.

The shifting upward of the mammillary processes in the anal region is a specialization that has developed gradually in the Cetacea. It gives a longer lever-arm to the tendons of the *longissimus* and *transverso-spinalis* inserted into these vertebrae, which produces a higher efficiency of these muscles. The above-mentioned fact, that the small dolphins can attain almost the same speed as the large whales, may be ascribed not only to the laminar flow of the water along their body, but at least also partly to this higher efficiency of their spinal musculature.

In the present state of our knowledge this explanation of the remarkable swimming speed of dolphins is however only a supposition. Careful researches on the intimate structure of the spinal musculature and on the forces exerted on the skeleton by these muscles must be carried out before better insight into this question can be achieved.

SUMMARY

The present state of our knowledge of the locomotion and the locomotory organs in Cetacea is reviewed.

The results of experiments on the flexibility of the body of the Common Porpoise have been confirmed by films of swimming Bottle-nosed Dolphins and a Pigmy Sperm Whale.

Cruising speed and maximum speed appear to be almost the same in the small dolphins as in the big whales. This phenomenon can be explained by assuming that the flow of the water along the body of the dolphins is wholly laminar, but that it is partly turbulent in whales. Another plausible explanation is furnished by the supposition that in dolphins the development and the insertion of the spinal musculature shows a higher degree of efficiency than in whalebone whales, as may be deduced from the shifting upward of the mammillary processes of the posterior lumbar and the anterior caudal region in dolphins.

The development of the muscles and the insertion of the tendons is adapted to the presence of two centres of extreme mobility, viz. : at the anal region and at the junction of the peduncle of the tail and the flukes.

REFERENCES

Andrews, R. C. (1914). Monographs of the Pacific Cetacea II, the sei whale. *Mem. Amer. Mus. nat. Hist.* n.s. **1** : 293.

Backhouse, K. M. (1960). Locomotion and direction-finding in whales and dolphins. *New Scient.* **7** : 26.

Colam, J. B. & Hill, A. V. (1950). The horsepower of a whale. *Discovery* **11** : 374.

Gray, J. (1936). Studies in animal locomotion VI ; The propulsive powers of the dolphin. *J. exp. Biol.* **13** : 192.

Gray, J. & Parry, D. A. (1948). Aspects of the locomotion of whales. *Nature, Lond.* **161** : 191.

Gunter, G. (1943). The swimming speed of the bottlenose dolphin. *J. Mammal.* **14** : 521.

Gunther, E. R. (1949). The habits of fin whales. *Discovery Rep.* **25** : 113.

Hayes, W. D. (1953). Wave riding of dolphins. *Nature, Lond.* **172** : 1060.

Kermack, K. A. (1948). The propulsive powers of blue and fin whales. *J. exp. Biol.* **25** : 237.

Lane, F. W. (1953). Speed of dolphins. *J. Mammal.* **24** : 293.

Layne, J. W. (1958). Observations on freshwater dolphins in the upper Amazon. *J. Mammal.* **39** : 1.

Parry, D. A. (1949). The swimming of whales and a discussion of Gray's paradox. *J. exp. Biol.* **26** : 24.

Parry, D. A. (1949) The anatomical basis of swimming in whales. *Proc. zool. Soc. Lond.* **119** : 49.

Roux, W. (1883). Beiträge zur Morphologie der funktionellen Anpassung. 1. Structur eines hochdifferenzierten bindegewebigen Organes (der Schwanzflosse des Delphins). *Arch. Anat. Phys.* **1183** ; Anat. Abt. : 76.

Scholander, P. F. (1960). Wave-riding dolphins : How do they do it ? *Science* **129** : 1085 ; *Norsk. Hvalf. Tid.* **49** : 265.

Slijper, E. J. (1936). Die Cetaceen, vergleichend anatomisch und systematisch. Diss. Utrecht ; *Capita Zool.* **7** : 1.

Slijper, E. J. (1946). Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. *Verh. K. Ned. Akad. Wet.* Afd. Natuurk. (2) **42** : No. 5.

Slijper, E. J. (1958). *Walvissen,* Amsterdam. (An English translation published by Hutchinson's—London is announced to appear in 1961).

Steven, G. A. (1950). Swimming of dolphins. *Science Progr.* **151** : 524.

Woodcock, A. H. (1948). The swimming of dolphins. *Nature, Lond.* **161** : 602.

Woodcock, A. H. & Macbride, A. F. (1951). Wave-riding dolphins. *J. exp. Biol.* **28** : 215.

GENERAL DISCUSSION

Chairman : Professor Sir James Gray, C.B.E., F.R.S.

A speaker asked if the function of the "melon" on the porpoise and dolphin could be to provide a lift of the head, counteracting the apparently excessive power of the upstroke in the tail.

Dr Slijper doubted the asymmetry of the power stroke, pointing out that hypaxial and epaxial musculature were almost equally developed.

Dr Manton mentioned Dr Hill's contention that inertia could be an important factor in swimming speeds. The weight ratio of whale to porpoise was 1000 to 1, and the greater inertia of the larger animal, leading to a tail beat which is about one tenth as fast in the whale, could be responsible for the relatively slower speed of this animal. In smaller animals the inertia effect is apparently negligible. The speed of running of diplopods where the movement of the limbs is not very fast, is almost proportional to their length, over a weight range of 6000 to 1. Centipedes on the other hand do not increase their speed in proportion to their length.

Dr Slijper doubted whether the frequency of beat in the large whales differed so much from that in the porpoise, and pointed out that in terrestrial mammals, the large animals were capable of much higher speeds than the small ones.

THE POWER REQUIREMENTS OF BIRDS IN FLIGHT

BY

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Within the last fifty years there have been many attempts to estimate the energy used by birds in flight. Such estimations present great problems, particularly since no direct approach is possible.

Several lines of attack are possible. One can measure the aerodynamic properties of birds' wings under controlled conditions in a wind tunnel. This can give some indication of the conditions in gliding flight, but with unknown and possibly large inaccuracies due, amongst other factors, to the absence of a functional intrinsic musculature. Attempts can be made to build from this information a theoretical flapping system by a point to point summation of a series of attitudes of the wing chosen to represent a flapping cycle. This involves a simplification of the complex change of shape and velocity of the living wing, and again introduces unknown inaccuracies. One can also approach the problem by a different route. By measurements or estimates of the metabolic rate, oxygen, or food consumption one can attempt to evaluate the power available from the muscles. One has to make some more or less arbitrary allowance for the efficiency—i.e. how much of the energy released from the food is made available for external work. One can take the figures which have been obtained for the power output per unit weight of mammalian muscles, apply them to the bird, and see whether reasonable aerodynamic properties can be predicted. All these methods have been tried at various times, and, while in no case has an unambiguous result been achieved, one can combine the figures from different authors and at least obtain some interesting information.

The first real attack on the problem came from Lilienthal (1911). He began by studying the air reaction on flat and curved surfaces presented to the air stream at varying angles. With this information he attempted to synthesize the flight of the stork in the following way. He considered the wing as being made up of four sections along its length. He assumed that the two sections nearest the body would have no important increase in velocity due to the wing beat, and would provide only a lifting force on both up and down beats. He assumed a forward speed of 10 metres a second, and a fixed amplitude of beat, and then calculated the absolute paths and velocities of the different sections through the air. From his experimental figures he determined the vertical and horizontal forces to be expected for different angles of the parts during the up and down strokes. From the tables so compiled he selected a set of suitable angles for the parts of the wings on the up stroke, and another set for the down stroke. By adding the four sets of vertical and horizontal forces from the parts over the period of a complete wing beat he was able to estimate the power required to maintain flight. In this model, based on a simple vertical

line of beat, he could not find conditions where the weight of the body was fully supported during the upstroke. As a result his model predicted a loss of both height and speed during the up stroke which had to be regained on the down stroke. In these conditions he calculated a power requirement which is equivalent to about 0·08 horse power per pound weight of muscle in a bird weighing some nine pounds. He points out that the bird may improve the efficiency by flexure of the wing tip on the up stroke.

Gnosspelius (1925) attempted a similar synthesis. He assumed aerodynamic properties similar to those of a well-known wing section, R.A.F. 15, and concluded that Lilienthal's stork should require an output of 0·04 horse power per pound of muscle. He suggested that this figure was too high to be possible. Then Walker (1925) examined a theoretical system with a more complex wing whose section was not constant along the span, and which had a higher velocity of vertical flapping on the up stroke and on the down stroke. While his model could never take off—a horizontal velocity was necessary in his treatment—nevertheless level flight was theoretically achieved. When he calculated the flight performance of a rook with the properties of his model he found that it required an output from the muscles of about 0·03 horse power per pound.

The next approach came from Boel (1929). His method was to take as an example a condor weighing twenty-two pounds, and to assume that at a speed of 50 feet per second, the lift force was 20 times the drag force on the whole animal. His calculations were then carried out as follows. Since the lift must equal the weight W in level flight, then the drag D must equal the lift divided by the lift to drag ratio,
or

$$D=\frac{W}{L/D}$$

and, since the power required is equal to the drag $D\times$ the velocity V then

$$P=\frac{W}{L/D}\times V$$

for the condor $P=\frac{22}{20}\times 50=55$ foot pounds per second.

A twenty-two pound bird will have about two and a half to three pounds of flight muscle, which must therefore produce about 0·4 horse power per pound.

Boel also applied this method to measurements made in a wind tunnel by Naylor & Simmons (1921) on a stuffed swallow. From the figures they obtained for lift and drag, and estimates from other sources of the weight of the species he calculated the minimum power for flight at various speeds. He found that the minimum power was 0·45 foot pounds per second, or 0·0008 horse power. The flight muscles weigh not more than 0·0125 pounds, and so would have to deliver some 0·064 horse power per pound.

There is a well established figure of 0·01 horse power per pound for the output of mamalian muscle during a sustained effort. If the swallow is assumed

to be capable of a similar output, then the calculations above suggest a power which is some six times too large.

One can tackle the general problem by starting from this mammalian figure and determining the properties that a bird would have to have to be able to use such an output. In a given species where one knows the weight of flight muscle one can obtain a figure for the available power. Then one can proceed as follows :—

$$\text{Power } P = \text{Drag } D \times \text{Velocity } V$$

or

$$D = P/V \qquad (1)$$

Also

$$\text{Lift } L = \text{Weight } W \text{ (in level flight)} \qquad (2)$$

Therefore

$$L/D = W \times V/P.$$

For a swallow flying at 50 feet per second—34 miles an hour—(not an unreasonable speed) we obtain a lift to drag ratio of 36 which is very high. Similar calculations for a pigeon give an L/D ratio of 35. Both these figures are at least unlikely. They certainly cannot be achieved in a model of comparable size. It must be remembered, moreover, that this is an estimate of conditions in level flight only.

During climbing or accelerating the rate of consumption of energy will be greater and may be many times greater than that required in level flight.

At this stage we can come to no definite conclusion. It is clear that if we assume a muscle power similar to that of the mammal then we must require an aerodynamic system with a L/D ratio substantially higher than we can achieve in man-made devices. Must we then look for something peculiar in the properties of feathers, or in the properties of the complex flexible wing, or perhaps for some unexpected advantages in flapping movements ? On the other hand we might suggest that the various calculations, due to Lilienthal and others, which show a surprising agreement on the power required, are correct. It would follow then that the bird muscle must be very different from its mammalian counterpart, and capable of making energy available for external work at a rate at least five times greater.

In recent years some more information has become available which goes a long way towards solving the problem. Pearson (1950) obtained figures for the oxygen consumption of humming birds. The resting metabolism required about 15 ccs. of oxygen per gram body weight per hour. During flight the rate increased to 80 cc./gm./hr. If all this excess is to be attributed to the requirements of flight, and if, as Pearson suggests, it is used in the oxidation of fat, it represents an output of 0·0008 horse power per gram body weight. According to Pearson's figures the bird weighs three grams ; from Savile (1950) the flight muscle is one-third of the body weight or one gram. These muscles are therefore achieving a rate of energy release equal to 0·36 horse power per pound—thirty-six times the power available from mammalian muscles. This estimate of course gives no information on the power actually available. Zeuthen (1942), assuming certain aerodynamic parameters and an energy

transfer efficiency of 25 per cent from the muscles, concluded that a pigeon flying at 43 miles per hour required a comparable rate of energy production from the muscles. If these estimates are correct then one can postulate an aerodynamic system which is not exceptional, If we accept Zeuthen's figure of 25 per cent efficiency, and Pearson's figure for the energy release within the muscle, then we can allow about 0·09 horse power per pound of muscle. This would provide more than enough power for flight of the type postulated by Lilienthal or Walker. But does the bird in fact need as much power ?

There is one source of data on the aerodynamic characteristics of a particular bird. Raspet (1950) was able to measure the performance of a gliding vulture (*Coragyps*). His method was entirely different from anything previously tried. He followed a gliding bird in a sailplane whose performance was accurately known. By filming the bird with a camera fixed to his machine he was able to determine the difference between its gliding angle and the known gliding angle of the sailplane at the particular speed. The data obtained showed a maximum L/D (minimum gliding angle) of 22 to 1. Since the wing area is very large, the lift per unit area is small, and therefore the drag must also be very small. The surprising fact which emerges is that the drag is actually close to the minimum possible drag of a smooth flat plate. Even so, and assuming that the efficiency in flapping flight is no less, if the bird is to maintain itself in level flight it will require an output of 0·02 horse power from its muscles. According to Raspet his bird weighed 5·1 pounds. The flight muscles would be about one-eighth of this or 0·64 pounds ; they must therefore have an output of about 0·03 horse power per pound.

We have now surveyed all the existing information. Can we come to any definite conclusions ? The aeronautical engineers have given estimates based on theoretical treatments of flapping systems using aerofoil sections with known properties. These suggest minimum muscle powers of 0·03–0·06 horse power per pound in level flight, but is it unreasonable to expect that the birds in millions of years may have evolved more efficient wings than we have ourselves developed in the last fifty years. In particular we now know enough to realize that a rigid mathematical treatment of these small flexible wings with their complex changes of shape and attitude in flight is not feasible ; and that attempts to simplify the pattern in order to make a solution possible can lead to gross errors.

We know from experiments on the metabolic rates of flying insects, Weis-Fogh (1956), that energy releases in the muscles may be as much as 400 kcal./kgm./hr., or in our units 0·3 horse power per pound total body weight. As noted before, Pearson's figure for the flight metabolism of the humming bird is similar. With no accurate information on the efficiency of energy transfer of the muscles, we cannot hope to do more than make reasonable suggestions as to the amount of power actually being fed to the wing. From Raspet's work we have the only example where we can say, with confidence, what minimum power a particular bird requires in flight. Again we find the figure of 0·03 horse power per pound of muscle. It must be remembered that the condor is a bird which does not carry out powered flight to any great extent, and its muscles are small. It may be that here the muscles may be required

to produce a higher output than would be permissible in the muscles of a bird which undertakes long duration flights without gliding. Certainly if similar frictional drag—drag appropriate to laminar flow over most of the wings and body—can be postulated for smaller birds with their relatively larger muscles, the energy outputs postulated from the metabolic studies are more than adequate. The most one can say with confidence is that, while the evidence suggests that the aerodynamic efficiency may be higher than might be expected, at the same time the energy release in the muscles is certainly higher than that found in non-flying animals.

REFERENCES

Boel, M. (1929). Scientific studies of natural flight. *Trans. Amer. Soc. mech. Engrs* **51** : 217–242.

Gnosspelius, O. G. (1925). Notes on a paper by J. D. Fullerton " Flight of Birds ". *J. Roy. aero. Soc.* **29** : 543–47.

Lilienthal, O. (1911). *Bird flight as a basis for aviation.* London.

Naylor, G. L. & Simons, L. F. G. (1921). Experiments in a wind channel with an Alsatian swift. *Reports & Memoranda* (*A.R.C.*) 708.

Pearson, O. P. (1950). The metabolism of humming birds. *Condor* **52** : 145–152.

Savile, D.B.O. (1950). The flight mechanism of swifts and humming birds. *Auk* **67**: 499-504.

Raspet, G. (1950). Performance measurements of a soaring bird. *Gliding* **6** : 145–151.

Walker, G. T. (1927). Flapping flight of birds. Part 2. *J. Roy. aero. Soc.* **31** : 337–342.

Weis-Fogh, T. & Jensen, M. (1956). Biology and physics of locust flight. 1. Basic principles in insect flight. A critical review. *Phil. Trans. Roy. Soc.* (B) **239** : 415–458.

Zeuthen, E. (1942). The ventilation of the respiratory tract in birds. *Biol. Medd. K. Danske Videnks. Selskab* **17** : 1–50.

ASPECTS OF EQUINE AND CANINE LOCOMOTION

BY

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The locomotory tissues, bone, joint and muscle, are organized for particular purposes in keeping with the known habit of the species. Reference is made to the locomotory cycle of the dog and the value of sub-dividing the stages towards an analysis of examples of combined activity during movement, with the help of cine camera frames and observations from dissections of specially injected specimens. Experimental surgery can be used to test the theses postulated, and in this survey of selected areas of the limb particular attention is paid to accommodatory structures which help to maintain normal progression. Reference is also made to the gliding movement of the scapula in non-clavicular animals, well shown in the horse, and finally to features of the horse which are associated with its power of endurance and the ability to stand for long periods without strain.

As is well known, the locomotory act—be it in vertebrate or invertebrate, performed in the air, on or under the sea, or on the land—must subscribe to a set of physical principles. The will to move requires a properly organized arrangement of tissues controlled by the senses ; the method varies with the class of animal and species—a fact of evolution.

This act has engaged the attention of scientists throughout the ages since Borelli set the stage three centuries ago with his classical work " *De motu animalium* ". The evergreen reference, John Hunter, added his contribution and, thinking particularly of the mammal, the names of Strasser, Steindler, Elftmann, Manter come to mind. James Gray, to whom members of this Society in general and of this symposium in particular owe so much, has dealt with many classes and his " Studies in the mechanics of the tetrapod skeleton " (1944) is a valuable guide in which he has stressed the need to consider any locomotory machine as part of a complete functional unit. More anatomically Wood Jones has dealt with principles, and Colin Mackenzie with the action of muscles in normality and recovery from injury, while the only veterinarian who has considered this in some detail on the horse is Frederick Smith. Of the many physiologists it must be remembered that following the intial lead from Marey the camera was introduced, and the famous account of Muybridge, "Animals in motion ", first published in 1899, is still a book to be read by all students of animal locomotion. Finally in retrospect there are the Croonian lectures delivered in 1903 by Beevor on " Muscular movements ".

Considering the domestic animals, and features of other species only if they illustrate a principle, confining remarks to functional anatomical observations of how parts of a horse and dog move, with no reference to histology and little to mechanical principles, the following can be said by way of overall impressions of tissues working in combined activity. With bones and joints their symmetry is to be noted, the shoulder and hip moulded for action ; in that connection excellent examples are shown in the patellae and the carpus

and tarsus which subscribe at half-way limb level in long-legged mammals to the mass of long bone and muscle proximally and the arrangement of the digital formula distally. Again on symmetry there is the problem of radio ulnar movement, possible pronation and supination, and whether or not this is valuable ; similarly tibio-fibular mobility, which has been studied by many including Barnett & Napier (1953). The locomotory feature of ligament, a tissue very similar in structure to tendon, is that although exhibiting no motive power it has marked activity in guiding or even checking. There is to be noted that some lateral ligaments are attached excentrically to the axis of movement and therefore when the joint acts tension is produced on the " snap-joint " principle, an example of which is shown in the elbow joint of the horse.

Muscle, its anatomy in relation to movement and posture, has recently been reviewed by Lockhart in Bourne's " Structure and function of muscle " (1960), in which he discusses design, fibre, tendon, contraction, tone, tension, power, and examples from studies of the living human subject. This work follows the pattern of a previous survey by Colin Mackenzie (1945) which initially is concerned with principles. Mackenzie, however, was a little more mechanical in approach, and in addition dealt with the evolution of muscle action, re-education and rest, with examples from comparative anatomical studies. His work is basically for the surgical anatomist and in it he stresses a direct challenge to what is meant by " paralysis ". Are there not, for example, other structures which will maintain function of a part if a major unit is put out of commission, possibly masking the expected effect of paralysis ? One is trained, quite rightly, to avoid over-stressing the action of individual muscles and it is an established fact, which will be confirmed by clinicians in the human medical and veterinary fields, that even if large muscles are put out of commission immediate accommodation—sometimes excellent and as efficient as the normal—is made by others, so that any change of gait is negligible if present at all, a perfect example of combined activity. In other cases, as will be referred to later, change of gait or action is effected by the loss of a single large unit, but that is associated with the severity and nature of the interference.

Before reviewing such examples in the dog, consider the normal cycle. At the walk during each locomotory cycle, the limbs of any four-legged domestic animal pass through two phases: a phase of elevation or protraction when the limb is airborne moving forward on the body, and a phase of contact or retraction when the body moves forward on the grounded limb. Each phase can be further subdivided into three periods. Thus during protraction from full retraction, using the fore limb of the dog as an example (Fig. 1), the limb must first flex limb joints, then swing cranially, and then extend. The pictures shown are taken at 24 frames per second, and of the nine frames on Fig. 1, three for each period, (A, B, C) two are repeated therefore there are seven frames representing approximately a quarter of a second in time. There are at times during the phases and periods overlaps of activity and this is demonstrable pictorially, but it is reasonable for purposes of description to talk about activity within a set period. So far as the fore limb of the dog is concerned, during the period of limb flexion it is noted that carpus and elbow approximate in scissor-like fashion (Fig. 1 A) ; shoulder flexion is less obvious pictorially,

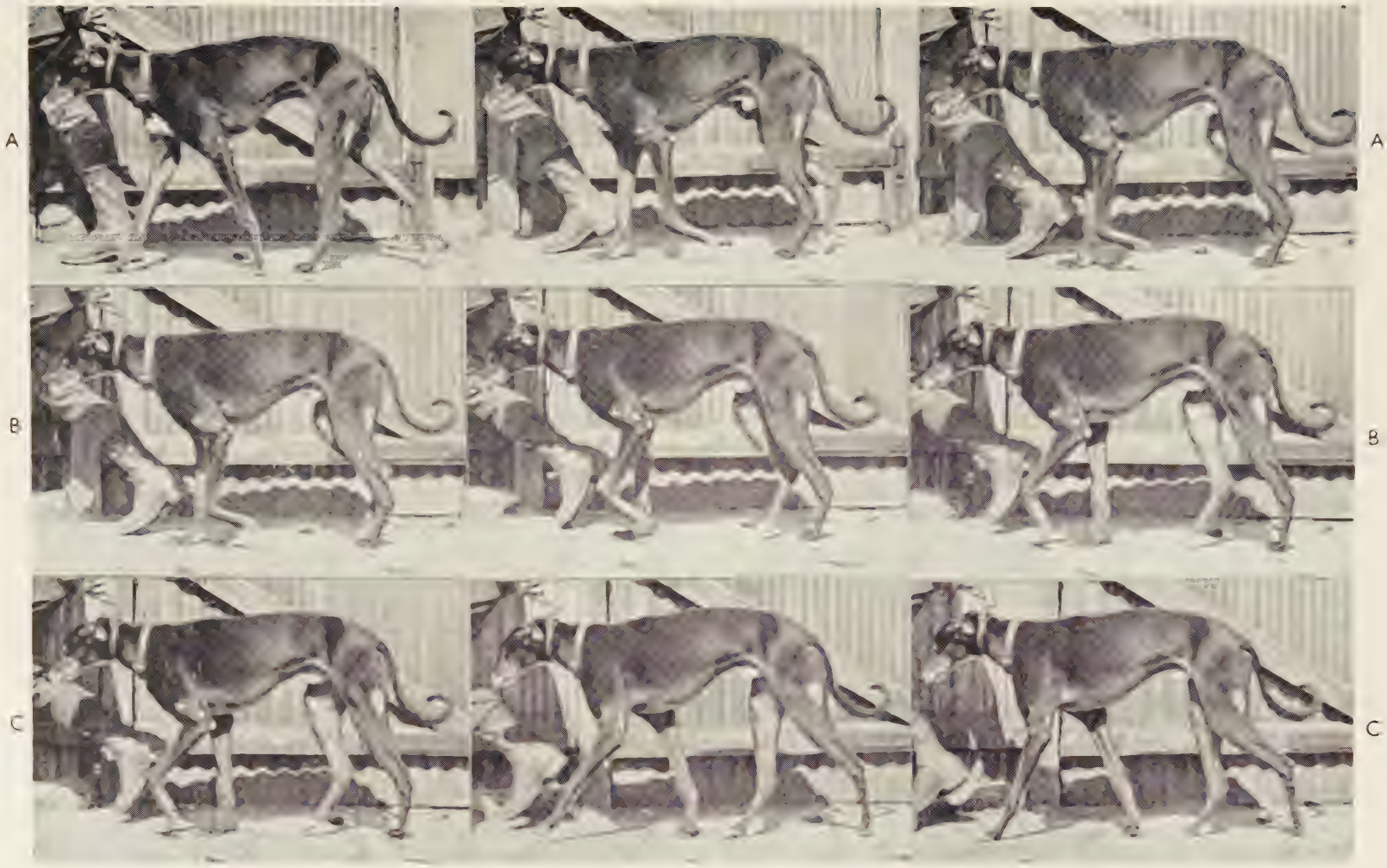

Fig. 1—Phase of elevation or protraction of the left fore limb of the dog : (A) Period of flexion ; (B) Period of cranial rotation ; (C) Period of extension.

Fig. 2.—Phase of contact or retraction of the left fore limb of the dog showing periods of first contact, maximum weight-bearing, and propulsion—three frames in each case.

the joint being so near the chest wall. During cranial rotation (Fig. 1 B)—the word " rotation " used as relating to the sagittal plane—the major limb joints are fixed and movement is confined to a swing forward of the shoulder (and therefore to protraction of the limb as a whole) on the body at the scaulo-thoracic junction ; while during extension (Fig. 1 C), made more efficient by the now more forward position of the limb, first the distal joints, then the elbow, and finally the shoulder extend. Only in the last stage of extension of the shoulder joint does the scapula move forward anti-clockwise on the humerus ; previously extension has been due more to clockwise movement of the humerus. The limb is now well-positioned to receive weight.

Throughout the three periods of contact the limb is engaged (Fig. 2), during the first period in accommodating to impact with the ground or attenuating concussion, this latter a most apt expression first used by the French anatomists Goubaux & Barrier in 1892 for this most important stage of the cycle, during the second period in receiving main weight-bearing when the limb passes over the vertical, and propelling in the third. During this period of propulsion, not strong in the fore limb as it acts more as a prop, all limb joints become extended as much as possible in retraction. The value of so dividing the phase of contact or support is seen if reference is made to the forces involved, which the pictures confirm. According to Oliver Barclay (1953 and a personal communication) the vertical forces (weight) increase as the limb passes from the state of full protraction to that when the main axis of the limb is at the vertical, are maintained at that level for a short time, to fall as the limb approaches full retraction ; whereas the horizontal forces (propelling power plus or minus) are braking before the leg reaches vertical, propelling afterwards. Further, according to Barclay, in overall limb progression lateral or transverse vertical forces in either limb are not strong, and the same could be interpreted from Manter's (1938) findings. The main forces are obviously translated into forward and backward components, but on each foot-fall there is a slight roll of the body sideways, and this may be a factor which helps to counter lateral thrusts.

In the fore limb of the type of animal being considered there are two general factors associated with the cycle which might be featured. One is what has been referred to as a scapular glide, and the moving horse shows this well (Ottaway 1955). Within the set-up of a scapula positioned on the lateral chest wall, in vertical line with the more distal components of a weight-bearing limb, the arrangement of shoulder muscles is such that there is a possibility at any pace of the scapula moving forwards and backwards, as well as upwards and downwards, independently of but possibly synchronized with movement of the shoulder joint. This axis of movement of the scapula on the thorax in non-clavicular species presents a circling not dissimilar from that of a wheel, which is of locomotory value. Secondly, in the absence of a clavicle there is muscle adjustment also of locomotory interest ; for example the two parts of the brachio-cephalic muscle, which might be termed the cleido-mastoid and cleido-brachial of Man, form a continuous muscle and this is represented as a powerful protractor of the shoulder and therefore the limb (Fig. 3).

It might be asked what muscles are in prime activity during any or all of these stages, either small or larger groups, or indeed the sequence of action of all muscles. It is perhaps dangerous to consider one limb in isolation without regard to the rest of the body, or to put too much stress on activity in small areas. Nevertheless if an appreciation of combined activity of muscles is to be obtained such an approach is justifiable. From dissection of fresh limbs, those specially injected to allow freedom of movement (Ottaway 1946), and observations of living animals, some conclusions can be drawn. If following such deliberations animals are subjected to experimental surgery more information can be obtained. In analysing the results of such experiments attention is directed to the accommodation of units, as this is part of the story of cooperative effort when considering the anatomy of normal progression. Muscles of the fore limb can be divided into three overall groups : movers of the limb joints distal to the shoulder, movers of the shoulder joint, movers of the scapula on the scapulo-thoracic junction. Although experiments have been conducted on muscles in all these groups, in this paper records will be confined (with one exception) to an analysis of the activity of muscles situated distal to the shoulder. Here the major groups are flexors and extensors of the manus, the triceps group and the main flexors of the elbow (the biceps and brachialis), all members of which groups could come within the definition of " gait muscles". Considering the questions previously mentioned, symmetry, ligament arrangement, and muscle organization, what accommodation would be expected and what do the experiments show ?

Flexors. Following neurectomy of the median and ulnar nerves in mid-humeral region, where in the dog they run together, flexion of the elbow was accelerated and of the carpus retarded during the period of flexion, and metacarpal-phalangeal movement was incoordinated. During extension of the lower limb joints the limb was well advanced and the foot was placed on the ground in a state of hyper-extension (Fig. 4). Throughout retraction this state of excessive extension persisted and the propulsive effort was consequently hindered, but little direct accommodation was necessary. Some adjustment was noted in positioning of the scapula during these weight-bearing stages, and earlier it would appear that the elbow flexors accepted overall responsibility for flexing the carpus, as when the elbow is flexed the lower limb joints will also flex to a degree due in this instance to mechanical contraction or passive activity of those flexors attached to the humerus. The triceps, without any moderation from the flexors, was responsible for controlling the state of the elbow while the lower joints extend.

Extensors. Following neurectomy of the radial nerve in mid-humeral region, peripheral to the origin of branches to the triceps, central to the origin of branches to the extensors of the manus, during the phase of elevation flexion of the carpus was exaggerated and extension of the manus coincided in time with extension of the elbow, which was normal (Fig. 5), indicating the accommodating influence of the triceps, one of the major groups of the limb. At first contact the toe was more upright, but throughout retraction no marked abnormality was observed in the gait, particularly after the leg has passed the

Fig. 3—Line drawing of the brachio-cephalic muscle of the horse and the comparable muscle of Man (from Ellenberger-Baum, *Handbuch der Vergleichenden Anatomie der Haustiere*, 18th edition, 1943, Springer-Verlag, Berlin).

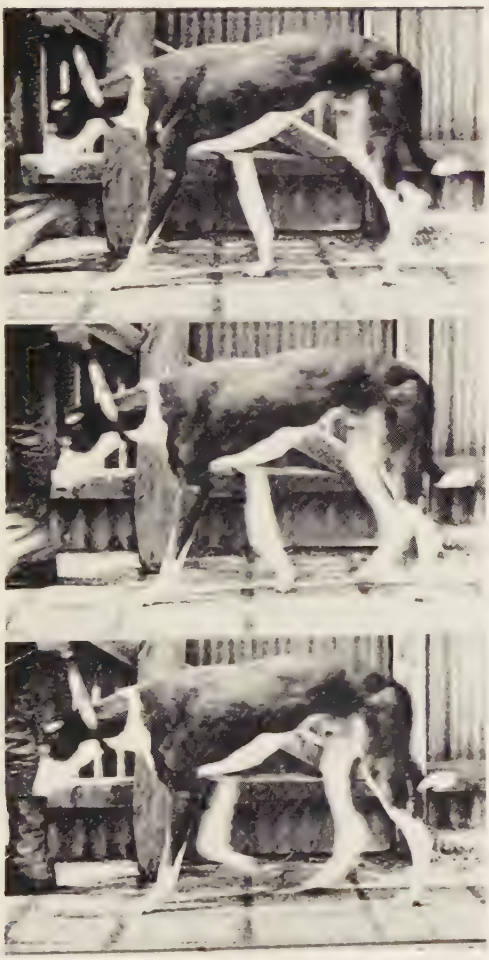

Fig. 4—The left fore limb of the dog during the first stage of contact following median and ulnar neurectomy.

Fig. 5—The left fore limb of the dog mid-way between the periods of cranial rotation and extension following radial neurectomy.

Fig. 6—The left fore limb of the dog following radial neurectomy at brachial plexus level (Worthman, 1957).

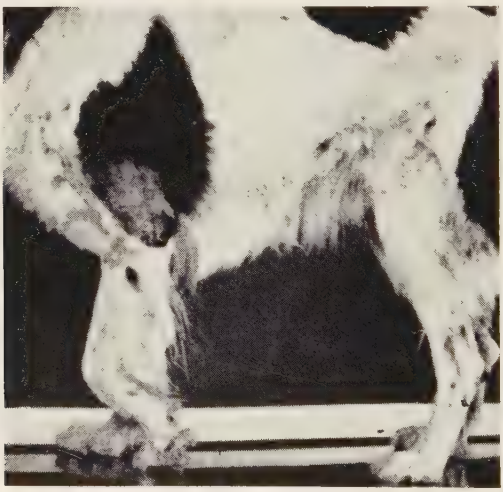

Fig. 7—The left fore limb of the dog following radial neurectomy distal to the branches which supply the triceps (Worthman, 1957).

Fig. 8—The left fore limb of the dog during the period of cranial rotation following tenotomy of the conjoined tendon of the biceps and brachialis.

Fig. 9 —The left fore limb of the dog during the period of extension following supra-scapular neurectomy.

vertical. When, however, in another experiment the combined triceps tendon was severed close to its insertion on the olecranon, a major loss, the effect was more severe, although the manus could be extended with difficulty. At rest the leg was held in a position typical of radial paralysis, suggesting the prime association of the triceps, the elbow extensor, with this affliction. Worthman (1957) records similar findings for radial neurectomy. He illustrates a case where the radial nerve was sectioned at brachial plexus level which demonstrates complete lack of control of the limb (Fig. 6) for, as he says, in this case both the triceps and extensors of the manus are out of commission. He rightly attributes the major loss to be the triceps, and in a case where the radial nerve was sectioned at mid-humeral level with the triceps still able to function, he shows that, although there is a tendency to knuckle over on to the dorsal side of the paw, limb extension is possible (Fig. 7).

Worthman also reported on section of the musculo-cutaneous nerve which supplies the biceps and brachialis (flexors of the elbow), and found that accommodation was straight-forward. This he attributed to the pronators and extensors of the manus acting atypically on the elbow. In an experiment similar to that of Worthman when the conjoined tendons of insertion of the brachialis and biceps were sectioned, flexion of the leg, which was minimal, centred on the shoulder and carpus, and there was little fixation of joints during the important period of swinging the leg forward prior to extension and contact as depicted in Fig. 8 ; nevertheless extension was effected without undue hindrance. In regard to flexion of the elbow following this operation it cannot be said it was strong or efficient, but it can be agreed with Worthman that such as was demonstrated was attributable to the pronators and to those extensors of the manus which take origin from the humerus. From the moment of contact and throughout retraction, lack of control of shoulder and elbow movement was observed, with alternating abduction and adduction of the elbow.

In regard to control of the final stage of extension of the shoulder, as already stated only approaching the conclusion does the scapula move forward, previously extension had been due more to clockwise movement of the humerus. There is no doubt that the supra-scapular muscles are involved in completing this act. The chief protractor of the limb is the brachio-cephalic, but, in the final stage of shoulder extension prior to accepting weight-bearing, it would appear that the supraspinatus muscle has an important part to play. In an experiment when the suprascapular nerve was sectioned, that complete extension which effects efficient positioning of the limb was hindered (Fig. 9). This last example relates to a small unit, but it is as important as the major groups in contributing to combined activity during limb progression.

From analysis of the results of these operations, chiefly on major units of the limb, added to preliminary observations, the following can be assessed as examples of combined activity and accommodation in movement of the fore limb of the dog in protraction. The flexors of the elbow are associated with the flexors of the manus, and in accommodation the triceps can also assist. The extensors of the manus are assisted by the triceps as extension of the elbow is a feature continuous with extension of the manus, and the triceps is the most

important single factor in this act. With the elbow flexors there is also a " stand-in " assistance or accommodation if necessary from those extensors of the manus which have a humeral attachment and from the pronators. As a further example of combined or multi-purpose activity of these groups it must be remembered that the long head of the triceps and the biceps brachii can influence movement of the shoulder as well as of the elbow.

Expressed in terms of sequence of the cycle relative to whole limb activity it can be estimated that, in the phase of elevation during the period of flexion, flexors of the manus commence the act ; their activity is followed immediately by the flexors of the elbow, which action also initiates overall protraction of the limb. Flexion of the shoulder follows that of the lower limb joints. With the limb fully clear of the ground all muscles below the shoulder fix to a varying degree throughout the period of cranial rotation, while prime activity in protracting the limb pivoting on the scapulo-thoracic junction is the concern of the scapular muscles. During the final period with the limb off the ground, initial extension commences with the manus extensors, tensed in the previous period—as a moderately fixed elbow is necessary for manus extension—this is quickly followed by contraction of the triceps in extending the elbow, with the brachio-cephalic and finally the shoulder extensors terminating the phase. In the support stages, during the first period flexors and extensors of the elbow are occupied with holding the state of the increasingly weight-bearing limb. Throughout the period of maximum weight-bearing, with the elbow moderately fixed, the extensors and flexors of the manus maintain tension, the flexors perhaps more so ; and during the final limb movement, with the shoulder now well forward, the elbow extends due primarily to contraction of the triceps. This may be called the period of propulsion, but as previously mentioned, the propulsive effort of the fore limb is not great. These are but limited functional anatomical observations ; the whole could be subjected to more critical analysis taking advantage of mechanical tests and more detailed examination of the tissues.

With the horse, the same sequence of limb movements takes place, but the interval between the stages varies both at the walk and more particularly at faster paces. Nevertheless a similar account of limb progression could be described. Two features of horse locomotion are worthy of note. By reputation this animal is able to endure and sustain a pace. Associated with this is muscle arrangement. The hip joint is presented as a deep socket well clothed by muscle, and of particular interest is the attachment of the biceps femoris muscle, which gains a sacral as well as dorsal pelvic origin. This former attachment is one of the most important factors in determining that vertebral movement of a moderately rigid back is uppermost at the lumbo-sacral junction, i.e. toward the pelvic limb. This is to be compared with the more spread mid-back movement exhibited in speedy but less sustained movers like carnivores. Figure 10, taken from Muybridge and used by Slijper, indicates back movement at speed. Add to this in the horse features of general size, the prow-like configuration of the chest, and the conformation of the fore limb allowing a good stride, and it may well be that these are high among the reasons why the horse has such powers of endurance.

The second feature relates to an equally well-known habit, the ability to stand at rest for long periods yet prepared to move. With the hind limb well-positioned under a sloping pelvis, stifle and tarsus flexed against gravity, an important feature which helps to maintain posture is the patellar lock described by Shuttleworth (1943) and commented on by Ottaway (1955). This, in fact, is the mechanism which, in virtue of the ligament and articular surface arrangments of the patella and femur, allows the patella to rest on an articular boss of the prominent medial lip of the femoral trochlea ; engagement and release being effected by muscles. Furthermore, in the horse as opposed to similar mammals, the fibularis (peroneus) tertius and the superficial digital flexor (plantaris) are tendinous and therefore mechanically control the synchronized

Fig. 10—An indication of mid-back movement in the carnivore and lumbo-sacral movement in the equine during the gallop (modified from Muybridge by Slijper).

movement, or state of rest, of stifle and tarsus : if one is fixed, so will be the other—a parallelogram of forces. To this could be added the rigidity of the mid-tarsal bones ; indeed in many horses of some breeds, without demonstrating any untoward symptom in life, many if not all of the mid-tarsal bones are fused. This, although strictly pathological and not often demonstrated in the riding-type horse, could be regarded as an ankylosis of locomotory value. As would be expected, the terminal parts of the major extensors and flexors distal to the tarsus are tendinous, but in addition the interosseous medius muscle of the single weight-bearing digit, the function of which—in both fore and hind limbs —is to help maintain the state of the fetlock joint, is replaced by tendon although in embryos and foals representation of muscle is found. This preponderance of tendon is of support value, and there can be few better examples in Nature of increased tendon-fibre and bone-ligament relationships allowing for relief of strain whilst standing, a habit exhibited by many horses for a large part of their life, yet all is ready for sustained movement.

In conclusion it can be said that this review has been selective, confined predominantly to the limbs and muscles, and little attempt has been made to introduce precise mechanical factors, although suggestions have been made. Nevertheless, it is hoped that all could be considered as within Gray's dictum of regarding the whole vertebrate body as a single mechanical system.

REFERENCES

Gray, J. (1944). Studies in the mechanics of the tetrapod skeleton. *J. exp. Biol.* **20** : 8–116.

Barnett, C. H., & Napier, J. R. (1953). The rotatory mobility of the fibula in eutherian mammals. *J. Anat., Lond.* **87** : 11.

Lockart, R. D. (1960). The anatomy of muscles and their relation to movement and posture. Chapter 1 in Bourne, G. H. (1960) *The structure and function of muscle* : 1 : *Structure.* New York and London : Academic Press.

Mackenzie, Sir Colin (1945). *The action of muscles.* 2nd edition. London : H. K. Lewis.

Barclay, O. R. (1953). Some aspects of the mechanics of mammalian locomotion. *J. exp. Biol.* **30** : 116–120.

Manter, J. T. (1938). The dynamics of quadrupedal walking. *J. exp. Biol.* **15** : 522–540.

Ottaway, C. W. (1955). Locomotion : the mechanism of movement. Chapter 14 in *Progress in the physiology of farm animals,* **2,** edited by John Hammond. London : Butterworths Scientific Publications.

Ottaway, C. W. (1946). A technique for the preservation of animals for the study of joint movement and for routine dissection. *J. Anat., Lond.* **80** : 207.

Shuttleworth, A. C. (1943). The function of the fermero-patellar joint of the horse. *J. roy. Army vet. Cps.* **15** : 2–7.

Worthman, R. P. (1957). Demonstration of specific nerve paralyses in the dog. *J. Amer. vet. med. Ass.* **131** : 174–178.

PREHENSILITY AND OPPOSABILITY IN THE HANDS OF PRIMATES

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CONTENTS

	Page
Introduction	115
Convergence-divergence	115
Prehensility	116
Opposability	118
Types of hand in living primates	
The convergent hand	121
The prehensile hand	123
Discussion	127
Acknowledgments	130
References	131
General discussion	131

INTRODUCTION

A prehensile hand with convergent fingers and an opposable thumb is a primate characteristic but is not a characteristic of all Primates. In some living Primates the hand is not even prehensile ; in some in which prehensility is present the thumb is not opposable, indeed in such as *Ateles* and *Colobus* an external thumb is altogether absent ; in some in which opposability is present, the perfected function of opposing the thumb and index finger, pulp-to-pulp, an action characteristic of *Homo* cannot be achieved. A wide variation of hand function can be seen in living Primates, from the convergent, non-prehensile hand of the *Tupaia* to the fully opposable hand of *Homo*.

There is no doubt that in this subject as in many others confusion and misunderstanding arises as much from semantic difficulties as from the inherent complexities of the subject. The purpose of this communication is firstly to discuss some of the terms used so freely in relation to hand function, e.g. convergence, prehension, opposition and opposability ; secondly to determine the anatomical basis of those functions in certain living Primates.

CONVERGENCE-DIVERGENCE

These terms denote the opposite extremes of a compound movement occurring at the metacarpo-phalangeal joints. Divergence consists of a fanning of the digits by means of extension and abduction ; convergence is the approximation of the tips of the digits and by means of a movement of flexion and adduction (Plate 1, fig. 1). All primate hands including that of man (Plate 1, fig. 2.), are capable of these movements. The ability to converge and diverge depends partly on the shape of the metacarpo-phalangeal joints but

primarily upon the presence of a transverse carpal arch. The arched form of the carpus is reflected in the arrangement of the metacarpals and the phalanges which are set upon a curve. The effect of this curvature upon a hand with a typical artiodactyl digital projection formula of 3> 4> 2> 5> 1 is to permit the digits to maintain contact with the ground during the stepping off phase of the walking cycle. In the absence of a carpal and metacarpal arch the contact of marginal and paraxial digits would successively be lost as the dominant axial digit became raised from the ground during walking.

Figure 1 (a) illustrates how digits set on a curve become adducted on flexion and abducted on extension.

Haines (1958) has shown how hands of a convergent type are associated with a particular arrangement of intrinsic musculature and he suggests that they are well suited to scrambling over rough ground and to climbing, when provided with sharp claws.

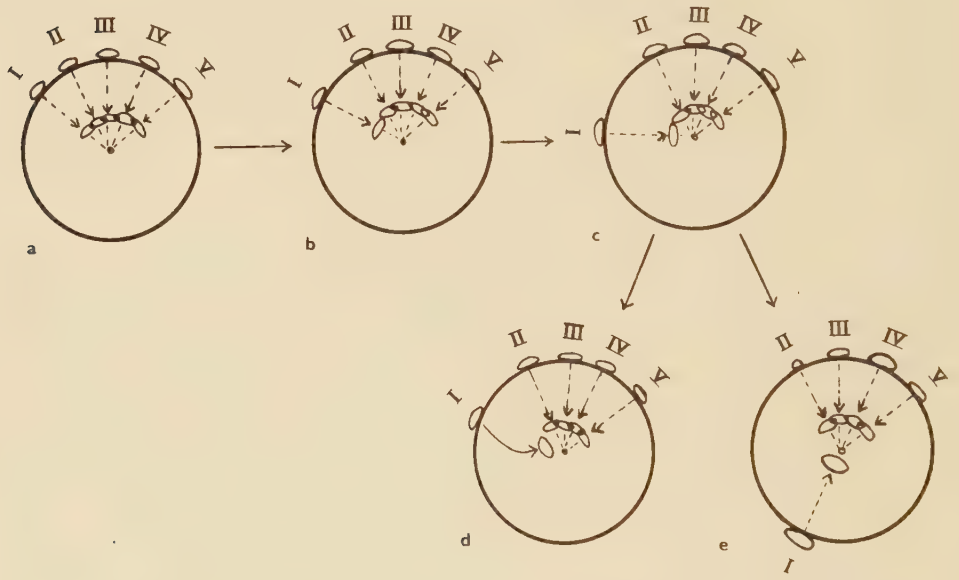

Fig. 1—a. Diagram of convergence of the digits in *Procyon*. b. Hypothetical condition in ancestral Primate showing convergence and prehensility. c. Convergence in a New World monkey (e.g. *Cebus*) with advanced pseudo-opposability. d. Convergence in an Old World monkey (e.g. *Papio*) showing true opposability. e. Convergence in lorisform (e.g. *Perodicticus*) showing an extreme example of pseudo-opposability. All the diagrams represent an end-on view of the tips of the digits. The small arrows within the circles indicate the line of the convergence. The larger arrows linking the circles indicate the general evolutionary trend.

PREHENSILITY

As has already been stated convergence is a basic function of the digits of all Primates. Prehensility is an expression of the effectiveness of convergence in terms of the hand as a whole in grasping. A convergent hand can be termed

prehensile when the digits approximate in such a manner that an object may be grasped and held securely *by one hand* against external influences (e.g. gravity) that may be tending to displace it. The prehensile grasp may be executed by an interaction of the digits alone or by the digits and the palm of the hand. In mammals in which the forelimb has become emancipated from a purely weight-bearing function, the behavioural correlate of this definition may probably be taken to be the presence of *habitual*, one-handed, hand-to-mouth feeding. Many rodents and some carnivores which employ the hands as aids to eating use a two-handed grip : the clamp action which is the essential mechanical basis of prehensility is achieved by these animals by employing both hands together.

The anatomical basis for prehensility, as has been suggested, rests upon the manner in which the digits converge in flexion, and this in turn depends upon the form of the carpal arch. The carpal arch is a generalized mammalian condition and is found in such forms as *Herpestes* (see Haines, 1958, Fig. 5) and in *Procyon lotor*. Its function is to enclose the long flexors of the digits ; its arched form is maintained by a fibrous sheet, the flexor retinaculum, which ties the two pillars of the arch together and converts it into a tunnel (the carpal tunnel). The depth of this tunnel depends upon the size and functional importance of the long flexors of the digits. In Primates for instance, the carpal arch is deepest in those forms in which finger flexion takes a dominant role in locomotion, and shallowest in those in which locomotion is of the more generalized quadrupedal type (Fig. 2). Thus in the capuchin, spider monkey, the colobus monkey, the Asian langurs and the anthropoid apes, the arch is deep ; in the guenons, macaques, sakis, uakaris and squirrel monkeys the arch is relatively shallow ; in man it is intermediate in depth.

The depth of the carpal arch appears to be produced on the radial side, by the orientation of the bones constituting the radial pillar of the arch, the trapezium and the scaphoid ; and on the ulnar side mainly by the size and prominence of the hook process of the hamate. As the arched form of the carpus becomes more pronounced so the orientation of the trapezium more nearly approaches a right angle relative to the plane of the dorsal surface of the capitate. In Primates with very deep carpal tunnels, the set of the trapezium clearly influences the set of the first metacarpal which thus becomes more in-turned as the tunnel becomes deeper. In Primates, it appears that the more locomotion depends on strong finger flexion, the deeper becomes the carpal tunnel and the more in-turned becomes the thumb. This is evident even in such forms as *Colobus* in which an external thumb is lacking but which retains a deep carpal tunnel.

Figure 1 (c) shows how prehensility is facilitated by an increase in the curvature of the carpus (and consequently, of the metacarpus and phalanges) ; flexion of the marginal digits in a plane at right angles to that of the middle digit in this example, which is typical of the arrangment in *Cebus*, results in them becoming *adducted relative to the hand as a whole*. The more in-turned is the pollex at rest the more adducted it will become when flexed. It is this change in the form of the carpus in response to the increasing demands of the flexor musculature of the digits that leads to prehensility, which in living

Primates is implemented mainly by the possession of an opposable or pseudo-opposable thumb.

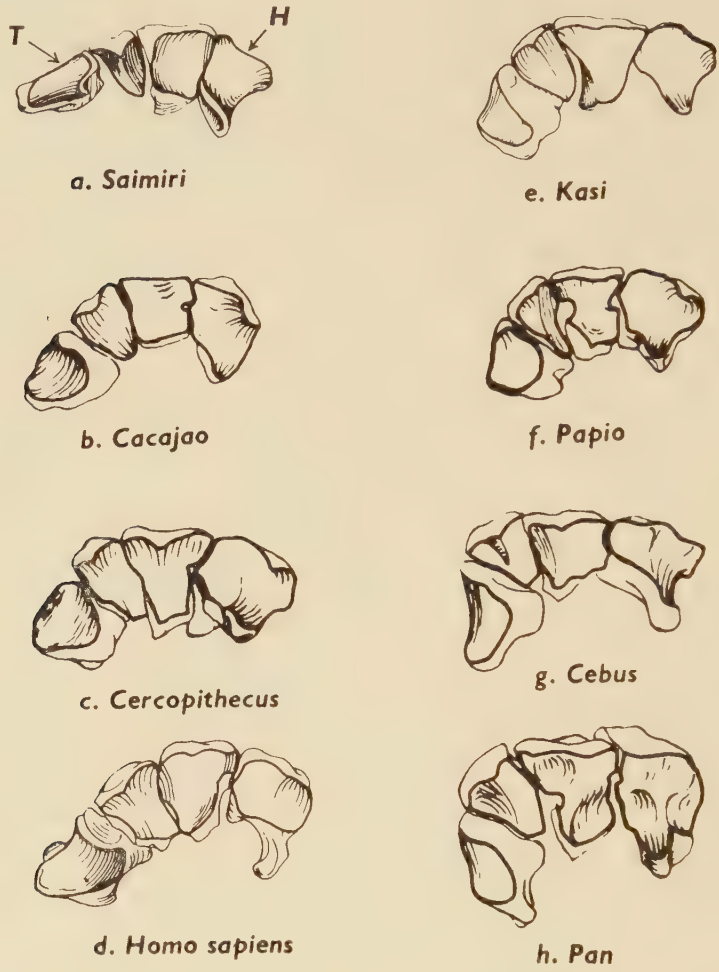

Fig. 2—The distal row of carpal bones of the left hand drawn from articulated specimens ; the surfaces for articulation with the metacarpals are shown. These diagrams demonstrate the variation in depth of the carpal tunnel in certain Primates.
T = Trapezium. H = Hamate. Drawn by Mrs Audrey Besterman.

OPPOSABILITY

Opposability is a form of prehensility in which the converging pollex undergoes an axial rotation so that at the end of the movement the thumb is facing towards the remaining digits (Fig. 1 e). It is clear that anatomists and zoologists have different ideas to the meaning of the term ; the former tend to regard it in a general sense of static oppositeness, and the latter in the more dynamic and precise sense of a particular movement which results in a particular function.

The carpo-metacarpal joint of an opposable pollex comprises a saddle articulation—a type of joint that has been discussed extensively, notably by Fick, L (1854) and Fick, R. (1911). The essential features of the joint are (1) that the articulating surfaces are reciprocally concavo-convex in their principle sections and (2) that in at least one plane there is a marked incongruity between the articulating surfaces in the mid-position of the joint (Fig. 3). These

Fig. 3—Diagrams of the first left carpo-metacarpal joint of man in longitudinal section through the bones in the abduction-adduction plane. Note the incongruity apparent in the mid-position. (Reproduced by kind permission of the Editor of the *Journal of Anatomy*.)

structural factors, given certain specific muscular and ligamentous arrangements (Haines, 1944, Napier, 1955) provide the basis of the compound movement of opposition that, on analysis, comprises a movement of abduction associated with flexion and medial rotation. In addition to the movement occurring at the carpo-metacarpal joint, opposability of the pollex in man and many Old World monkeys and apes is facilitated by an additional mechanism at the metacarpo-phalangeal joint whereby the proximal phalanx undergoes abduction flexion and medial rotation, thus substantially contributing to the ability of the thumb as a whole to face inwards towards the digits (Fig. 4 a). This movement has been discussed in earlier papers—in man (1952) and in chimpanzees and orangs (1960). In some Old World monkeys, e.g. *Macaca* a mechanism for further facilitating opposability is present in the terminal joint of the pollex where the articular surface of the proximal phalanx is tilted in a radial direction so that the terminal phalanx rests normally in slight abduction relative to the long axis of the pollex (Fig. 4 b).

It is clear that *opposability* is a function of the thumb as a whole rather than a movement of any individual joint. It should be stressed that *opposition* (the compound movement taking place at the carpo-metacarpal joint) is the principle mechanism by which opposability is achieved.

It may be appropriate to crystallize this general discussion by providing a definition for opposition : *opposition is a compound movement of abduction, flexion and medial rotation occurring at the carpo-metacarpal articulation of the pollex.*

In the sense of the foregoing definition only a certain number of Primates possess carpo-metacarpal opposition and these are all found among the Old World monkeys. New World monkeys do not possess opposition of the thumb in the anatomical sense of the word, although the thumb is capable of converging towards the remaining digits and, with them, forming a clamp. For opposability achieved in this or any way, other than by carpo-metacarpal opposition, the term *pseudo-opposability* is suggested.

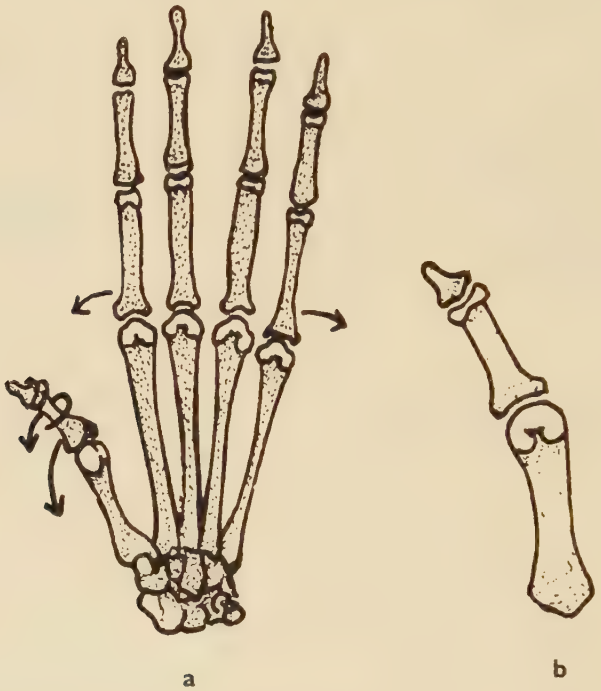

Fig. 4—a. Drawing of the left hand of a macaque monkey indicating, by means of curved pathways, the abduction and medial rotation movements possible at the first metacarpo-phalangeal joint. b. Drawing of the left thumb of a macaque to show the radial tilt of the distal articulation of the proximal phalanx and its effect on the set of the terminal phalanx.

Finally mention must be made of the perfected movement whereby the thumb and one or other of the remaining digits (usually the index finger) can be placed together in firm pulp-to-pulp contact (Plate 1, fig. 6). This function which provides the basis for skilled manual work can only be achieved in its perfected form in *Homo* and possibly only in *Homo sapiens*. The execution of perfect opposability depends on many neuro-muscular and sensory factors but ultimately rests upon the proportionate lengths of the thumb and index finger. Marked disproportion precludes proper apposition of the two digits. An extreme example of disproportion in catarrhines is shown by the orang-utan which, in association with its particular locomotor habit, has evolved a very short thumb and very long fingers. These animals have a saddle articulation at the carpo-metacarpal joint and have therefore the essential mechanism to

oppose, but the disproportion of the thumb and digits disbars effective opposability. Examples of less markedly disproportionate hands are found among the highly arboreal leaf-eating monkeys, whose mode of locomotion approaches the brachiators in its acrobatic qualities ; in these forms opposition is very imperfect. The macaques and cercopitheques whose locomotor activity is essentially quadrupedal, whether terrestrial or arboreal, have hands that in their proportion, approach the human pattern and, consequently, it is among these forms—particularly the terrestrial species—that the nearest approach to the human pattern of finger-thumb opposition is found.

TYPES OF HAND IN LIVING PRIMATES

The convergent hand

The form of the primitive eutherian forefoot is still in some doubt. Gidley (1919) in severely criticizing Matthew's (1904) theory of an arboreal origin for placentals, pointed out the incorrectness of Matthew's assumption that the relatively great divergence of the pollex in Palaeocene fauna betokened an opposable digit. Gidley stated divergence of the first digit was a primitive reptilian condition and that it was quite distinct from opposability ; he admitted, however, that it would be quite a short step for a divergent digit to be converted to an opposable one.

Gregory (1951) proposed the terrestrial insectivores *Echinosorex* or *Hylomys* as representative of the central type of placental mammal. Haines (1954, 1958) on the basis of the intrinsic muscles of the hand suggested that *Herpestes*, a generalized terrestrial carnivore, was a truer representative of the central type of mammal.

The common North American racoon *Procyon lotor*, provides a good example of a convergent hand (Plate 1). The racoons are terrestial, nocturnal hunters who sleep, breed and take refuge in trees. Their hands are used conjointly when moistening their food and feeding and they have a well-developed sensory function ; they are of the convergent-divergent type with short strongly clawed digits that show a generalized artiodactyl projection formula, e.g. 3> 4> 2> 5> 1. The palmar skin is confluent in keeping with its highly developed sensory function, and the remains of six palmar pads are apparent, the thenar pad being particularly small and the hypothenar pad particularly large. The first digit is not divergent but the first interdigital cleft is deeper than the fifth. The contrahens muscles are three in number, supplying digits I, II and V ; between contrahens I and contrahens V there is a raphé extending one-third of the length of the palm (Fig. 5 b). Contrahens II arises from this raphé. The contrahens V is the largest member of the series. Haines (1958) interprets raphé formation as evidence of arboreal adaptation. The contrahentes show no raphé formation in *Herpestes* (Fig. 5 a) but in a fully arboreal form such as *Trichosurus vulpecula* (Fig. 5 c) or *Didelphys virginiana* the raphé formation extends far distally into the palm. The presence of a short raphé in *Procyon* therefore may be taken as indicating some degree of arboreal specialization.

The raccoon provides a good example of a still fairly generalized mammal in the early stages of arboreal adaptation, annectant in a functional sense,

between the terrestrial *Herpestes* and the arboreal *Tupaia*. The hand of *Procyon* is fairly generalized in all but its sensory function ; it is convergent and non-prehensile.

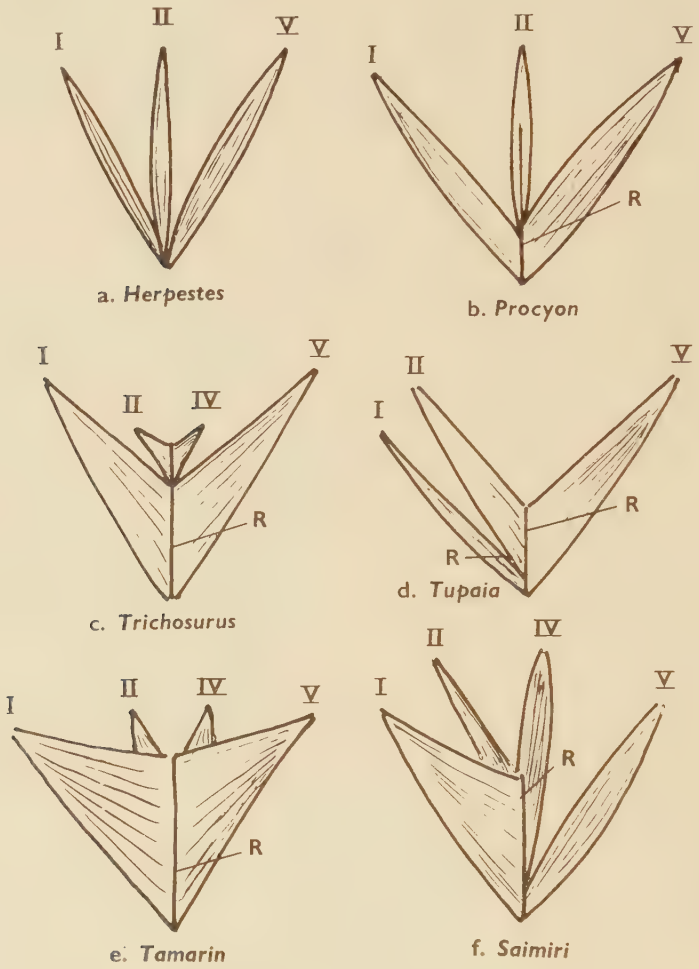

Fig. 5—The pattern of the contrahens muscles in a number of different mammalian genera. Fig. a is after Haines (1948) but Figs. b–f are drawn from original dissections.
R =raphé.

Tree-shrews are, generally speaking, arboreal animals although they are known to occupy a wide variety of forest zones from ground level, through the shrub layer of the forest floor to upper canopy levels (Le Gros Clark, 1927, Sanderson, 1957). The reports on the use of the hand in *Tupaia* during feeding are somewhat contradictory, it would appear (Le Gros Clark, 1927) to be mainly a two-handed feeder. The hands of *Tupaia* are elongated, the digits having the typical artiodactyl projection formula (Plate 1, fig. 4). Palmar pads are well differentiated and six in number. The digits are evenly spaced, the cleft between digits I and II being slightly deeper than that between

IV and V, as in *Procyon*. The pollex shows no external evidence of differentiation but during movement a particularly well marked divergence of the thumb is apparent ; it is clear from observations on the living that this movement is occurring at the metacarpo-phalangeal joint of the pollex and not at the carpo-metacarpal joint.

The flexor musculature in *Tupaia* consists of a flexor sublimis sending tendons to the medial four digits and a flexor profundus with five tendons, one to each digit, the bulk of the profundus tendons being several times greater than that of the sublimis (see Haines, 1955, Fig. 3). The flexor pollicis longus muscle is not discrete. The contrahentes are substantially as described by Haines (1955) consisting of three slips one each to digits I, II and V (Fig. 5 d) ; raphé formation is present between slips II and V but while longer than in *Procyon* it is not so extensive as in *Trichosurus*. There is a very short raphé between slips I and II but as Haines has stated the contrahens to the pollex is virtually independent. The carpal tunnel in *Tupaia* is deeper than in *Procyon* ; this observation is in keeping with the large size of the flexor digitorum profundus and the importance of claws in arboreal climbing.

Haines describes the carpo-metacarpal joint of the pollex as saddle shaped and it is clear that he regards this digit in *Tupaia* as in some measure opposable. Montagu (1960) describes the pollex as showing " some degree " of opposability ; but Le Gros Clark (1959) states that " observations on the living animal have shown that by a converging flexion movement [tree-shrews] can secure a strong grip of small objects ".

The carpo-metacarpal joint of the pollex is of a typical " hinge " variety. The essential feature of saddle joints—incongruity in one principle section—is absent (see Fig. 3). It is unlikely that any appreciable degree of axial rotation could occur at such a joint.

The hand of the tree-shrew is convergent (divergent when performing as a forefoot). The convergence is more highly developed than in *Procyon*, as witnessed by the arrangement of the contrahentes. In the absence of definite evidence of habitual one-handed feeding it should probably not be regarded as prehensile. There is some evidence however of the differentiation of the pollex foreshadowing, in the mobility of the metacarpo-phalangeal joint, the prehensile hand and pseudo-opposable thumb of *Tarsius*.

The prehensile hand

I. Pseudo-opposable

The tarsiers are nocturnal arboreal animals which progress from branch to branch by leaping and maintain their stability at rest frequently on a vertical stem by means of strong grasp of hands and feet.

The digits have a typical artiodactyl projection formula, their terminal pads are in the form of expanded discs which are covered with fine papillary lines ; the tips of the digits are backed by short, pointed true nails (Le Gros Clark, 1936). The first metacarpal is not divergent and the first interdigital cleft is only very slightly deeper than the cleft between digits IV and V.

The arrangement of the contrahentes differs somewhat from that described by Woollard (1925) but further dissections are necessary before the pattern can

be firmly established ; the form of the contrahens to the pollex, however, is unequivocal. It arises from a common raphé attached to the shaft of the third metacarpal and forms a large fleshy muscle (the biggest of the contrahens series) that in its form and attachment corresponds to the adductor pollicis of higher Primates ; it can be separated as Hill (1955) points out into oblique and transverse portions. In addition there is a separate slip, associated at its origin with the oblique head and passing laterally, deep to the flexor pollicis longus tendon, to be inserted into the radial side of the proximal phalanx of the thumb ; this slip probably corresponds to the deep head of flexor pollicis brevis in higher Primates (Day & Napier, 1961). As Hill (1955) points out the thenar muscles are quite well differentiated, particularly the abductor pollicis brevis which in one dissection could be separated into two parts and which are inserted very much as in man (Napier, 1952). The opponens pollicis as a functional entity is absent although a few of the fibres from the deep surface of flexor pollicis brevis reach the shaft of the first metacarpal for part of its length, as described by Woollard (1925).

The carpo-metacarpal joint of the pollex is of the " hinge " variety allowing flexion and extension ; there is a possibility that some abduction and adduction also occurs but, if so, the movement is very limited ; certainly no rotation is possible at this joint. The metacarpo-phalangeal joint of the pollex is condyloid and is freely moveable when examined, intact, in a wet specimen. The presence of a well developed abductor pollicis brevis and a deep head of flexor pollicis brevis are strong indications that abduction and rotation occur in the pollex. It is clear from the form of the carpo-metacarpal joint that no substantial range of abduction or rotation takes place at this level and therefore it can only be assumed that it is at the metacarpo-phalangeal joint that these movements are taking place. The absence of a well marked opponens pollicis adds further point to this view.

Observations on the opposability of the thumb during life in captivity are inconclusive. Pocock (1918) regarded the thumb as non-opposable. Le Gros Clark (1959) notes that the thumb possesses very little functional differentiation in movements of the hand. Polyak (1957) after considerable personal observation concluded that the movement is better regarded as abductability and adductability than opposability. A study of the many photographs of life studies of living tarsiers particularly those published by Polyak (see his Figs. 497–514) makes it quite clear that movements of abduction and rotation of the pollex occur, and that they are taking place at the metacarpo-phalangeal joint, and that little or no movement is occurring at the carpo-metacarpal joint (Fig. 4).

The hand of *Tarsius* therefore can be regarded as prehensile and the thumb as pseudo-opposable, a term which has been suggested for movements of the thumb which are attributable to movements other than carpo-metacarpal opposition (vide supra).

The Cebinae, the capuchins and squirrel monkeys, have a fairly generalized form of arboreal locomotion. Like all New World monkeys they are fully arboreal and progress by quadrupedal leaping and climbing. Their hands are pentadactyl, the projection formula of the digits is typically artiodactyl (but

sometimes 3=4 or 4>3 [Hill, 1960]). The nails show a transverse dorsal convexity but are true nails, the palmar skin is confluent and the pads not strongly defined. The thumb is poorly differentiated from the remaining digits ; the first interdigital cleft being only slightly deeper than the fifth. The pollex is not generally regarded as opposable (Pocock, 1925, Midlo, 1934, Hill, 1960).

Fig. 6—The distal articular surface of the distal row of the carpus of the Miocene species *Proconsul africanus*. (Napier & Davis, 1959). The broken lines indicate the reconstructed portions of the carpus. The set of the trapezium was established by reference to its articulation with the second metacarpal which was preserved.

The contrahentes according to Forster (1916) consist of a central raphé which provides attachment for a large contrahens I (adductor pollicis) and a small contrahens V, these two structures overlie the smaller contrahens muscles to II and IV. The thenar muscles are well differentiated and consist of an abductor and flexor pollicis brevis but no opponens pollicis. The true deep head of flexor pollicis brevis is absent (Day and Napier, in preparation).

The carpal tunnel is deep in *Cebus* but shallow in *Saimiri* (Fig. 2) ; in *Cebus* the set of the trapezium approaches a right angle while in *Saimiri* the set of the bone relative to the plane of the dorsal surface of the capitate makes an angle of about 35°. The carpo-metacarpal joint of the pollex in *Cebus* is one in which flexion and extension are freely permitted but in which a small amount of abduction and adduction can also occur ; axial rotation is not possible. This type of joint can only be referred to as a " modified hinge ", somewhat similar in its permitted movements to the humero-ulna joint of higher Primates.

Observations on living capuchins indicate that they are exceptionally dexterous but the thumb, nevertheless, is not fully differentiated. As in *Tarsius* the functional mobility of the pollex is attributable largely to the mobility of the metacarpo-phalangeal joint ; in the absence of true opposition at this joint, the movement of the thumb is classified as pseudo-opposable.

The form of the carpo-metacarpal joint in the Miocene fossil species *Proconsul africanus* is very similar to that found in *Cebus* (Napier & Davis, 1959) ; on reconstruction of the fossil hand the carpal tunnel appeared to be deep and the trapezium set at an angle of 90° to the plane of the dorsal surface of the capitate (Fig. 6). This angle of set is slightly greater than in *Cebus* but less than in *Pan* (Fig. 2). This particular feature of *Proconsul* taken in conjunction with many other features of the upper limb indicated that this Miocene hominoid incorporated a certain amount of brachiation in its locomotor pattern.

II. Opposable

The hand in a generalized Old World monkey can be distinguished from a New World form by the independence of the thumb, which as Midlo (1934) has shown, has migrated proximally ; as a result the thumb appears to be shorter relative to the index finger, and the first interdigital cleft deeper in catarrhines than in platyrrhines. In generalized arboreal forms such as

Fig. 7—A diagram of a first left metacarpal to demonstrate the twist of the head relative to the base.
A–B = transverse axis of the base of the bone ; C–D = transverse axis of the head.

Cercopithecus neglectus (De Brazza's monkey) and *Cercopithecus mona* (Mona monkey) the hand is pentadactyl with the primitive digital projection formula of 3> 4> 2> 5> 1. The skin of the palm is confluent and palmar pad remnants are quite well defined. The contrahentes to digits II, IV and V are much reduced, while contrahens I forms a well marked adductor pollicis. The remaining thenar muscles are well developed and there is a deep head to the flexor pollicis brevis. The carpal tunnel is moderately deep (Fig. 2) and the trapezium is set at approximately 50° to the plane of the dorsal surface of the capitate. The carpo-metacarpal joint is of the saddle variety being reciprocally concavo-convex ; the movements of the first metacarpal at this joint, therefore, include flexion-extension, abduction-adduction, and rotation. The composite movement of opposition effects an axial rotation of the thumb so that at the end of the movement the palmar surface is facing towards that of the remaining digits (Fig. 1 d). The metacarpo-phalangeal joint allows abduction and adduction as well as flexion and extension and, in addition, a certain amount of axial rotation which occurs at the end of abduction. Clearly

therefore, the thumb in these two species, as indeed in all living catarrhines* is opposable.

There is a considerable variation in the effectiveness of opposability, from a functional point of view among Old World Primates, the ability to place index finger and thumb in intimate pulp-to-pulp contact depending upon the relative proportion of these two digits. Opposability in perfected form is demonstrated by Man and in its least effective form among catarrhines possessing external thumbs, by the orang-utan. In general, as it has already been noted, opposability is more effective in terrestrial than in arboreal Primates.

Finally, mention must be made of a compensatory mechanism whereby the effect of a deep carpal tunnel is nullified by the presence of a lateral twist of the head of the first metacarpal relative to its base (Fig. 7). The anterior aspect of the base of the metacarpal, thus, corresponds to the angle of set of trapezium in the carpus while the head is twisted relatively laterally so that it is facing in a palmar (or plantar) direction. The twist is generally seen in Primates that combine a quadrupedal gait with the specialized arboreal locomotor patterns of brachiation and semi-brachiation† and, possibly, therefore may be regarded as a mechanism of compromise whereby a thumb—markedly in-turned as a result of a deep carpal tunnel is, at the same time, directed sufficiently plantarwards to meet the requirements of a plantigrade gait. In view of this possibility it is surprising that the twist is never exhibited by *Papio* a non-arboreal and habitually quadrupedal form in which the trapezium has an angle of set of approximately 80° (Fig. 2). It is possible that the absence of twist is related to the digitigrade gait of *Papio* which does not involve the thumb in weight bearing.

DISCUSSION

Unfortunately there is little in the way of fossil evidence of limb structure of ancestral Primates by which hypotheses relating to the structural and functional evolution can be supported. On the other hand, evolutionary studies of Primates are easier to pursue than those of other mammalian groups for the reason that living Primates constitute a graded series that approximates to the trend of primate evolution determined, for example, by cranial and dental palaeontology. Thus, it is possible to accept that homologous structures in a series composed of, for instance, tree shrews, tarsiers, New World and Old World monkeys, are likely to conform in a sequential but not necessarily consecutive manner to some of the stages of primate evolution. Care, however, must be taken to recognize specializations of structure in an otherwise generalized form that clearly break the sequence ; the form of the hand in anthropoid apes is the end result of a specialized line of brachiators and can in no way be regarded as part of the sequence in the evolution of the primate hand.

*The Hylobatinae have a carpo-metacarpal joint constructed on the ball and socket principle (Jouffroy and Lessertisseur, 1960) ; this arrangement is unique. The thumb, however, is opposable.

†The term semibrachiation has been devised by the author in association with Dr E. H. Ashton to describe the highly arboreal and acrobatic activities of certain of New and Old World monkeys. It replaces the term " generalized brachiation " previously used in this connexion by Napier and Davis (1959).

Evidence from comparative anatomy

The functions of convergence, prehensility with pseudo-opposable thumb and prehensility with an opposable thumb can be regarded as consecutive stages because there is evidence of even progression and overlap from one morphological type to the next. The convergent hand becomes increasingly convergent until it has reached the stage where it is convenient to refer to the hand as prehensile ; convergence is not lost as prehensility is achieved. The pollex of the prehensile hand becomes progressively more mobile and specialized ; this change is apparent initially at the metacarpo-phalangeal joint and, subsequently, as the carpal tunnel deepens in response to the demands of an increasingly prehensile hand, at the carpo-metacarpal joint. The movements at both these joints mimic opposability by deviating the thumb from the index finger and, to a varying extent, facing it towards the other digits. At the metacarpo-phalangeal joint, a pseudo-opposability is achieved by abduction, flexion and some terminal rotation taking place at the extreme range of abduction ; but at the carpo-metacarpal joint, which is of the hinge variety, flexion and abduction are sufficient in the presence of an in-turned trapezium to produce pseudo-opposability. It is at this point that a specialization mars the sequence ; true opposability results from an apparently sudden change in direction of evolution—the development of a saddle joint at the carpo-metacarpal articulation which permits a new movement to be added, that of metacarpal rotation. The main line of evolution possibly led to further and further divergence of the thumb and, consequently, to more and more effective pseudo-opposability until the perfect mechanical clamp (as seen in certain lorises (Plate 1, fig. 5), was evolved. The acquirement of true opposability does not mean that convergence is lost, nor that pseudo-opposability at the metacarpo-phalangeal joint is lost ; both these functions are absorbed into the more specialized hand of Old World monkeys, apes and man.

Haines, (1958) classified mammalian hand types as (i) convergent (ii) clamping (iii) opposable (iv) schizodactylous. In the present paper primate hands are classified as (i) convergent (ii) prehensile with pseudo-opposable thumbs (iii) prehensile with opposable thumbs. The differences between these two classifications are not as profound as they might appear and are mainly semantic. Haines includes *Tupaia*, here classified as convergent, in his opposable group on the basis of the independence of the first digit ; *Tupaia* certainly does not fit the opposable group as defined above ; in fact in the absence of definite information of one-handed feeding it is not even here regarded as prehensile. The independence of the contrahens to the pollex however, certainly suggests some differentiation of this digit which may well adumbrate the shift of functional emphasis to the radial side of the hand that is characteristic of the Primates as a whole. Differentiation of the thumb is not apparent in a convergent hand such as that of *Procyon* nor in the more specialized arboreal hand of *Trichosurus* which is also of the convergent type ; in *Trichosurus* the contrahens are more or less transversely directed and functionally both radial and ulnar borders of the hand receive equal emphasis. Haines has recognized this symmetry in structure and function by labelling this type of hand as " clasping ". No living primate demonstrates a clasping

hand although the marmosets approach it closely. In *Tamarin* the contrahentes I and V are transversely arranged but the contrahens to V is slightly smaller than that to I. This evidence of radial shift in muscle balance is echoed by the relative bulk of the abductors of the marginal digits, abductor pollicis brevis being slightly larger than abductor digiti minimi.

Haines includes certain platyrrhines such as *Cacajao* (Uakari) together with a number of marsupials in his schizodactylous group. Although in *Cacajao*, as in the sakis, the first and second digits frequently align themselves together for purposes of prehension, this function must be regarded as a behavioural mechanism that has been evolved to compensate for a somewhat ineffective thumb ; as already noted the carpal tunnel of *Cacajao* is very shallow (Fig. 2) and the trapezium, consequently, is not markedly in-turned. Although the hand of *Cacajao* is classified as pseudo-opposable along with the majority of New World monkeys, it is in no way as functionally effective as, for instance, it is in *Cebus*. A similar behavioural mechanism has been evolved quite separately by the orang-utan ; in the absence of effective opposability—due in this instance to a very short thumb and markedly elongated fingers—the orang frequently picks up objects between the second and third digits (Napier, 1960) (Plate 1. fig. 7.).

In the absence of any evidence that the pattern of contrahentes in *Cacajao* for instance is in any way similar to that seen in schizodactylous marsupial hands (e.g. *Pseudochirus*, *Phasacolarctos*, Haines, 1958), there is little justification for including this form in a special group.

In his opposable group Haines apparently includes all Primates not included in the schizodactylous group, e.g. lemurs, lorises, tarsiers (tentatively), Old and New World monkeys. His criteria for opposability, which are nowhere clearly expressed, do not take into account the nature of the carpo-metacarpal joint nor the possibility of movements occurring at the metacarpo-phalangeal joint. Thus, Haines' group of opposable hands can be equated with groups (ii) and (iii) in the present classification.

Palaeontological evidence

In spite of Matthew's (1904) belief, re-expressed in 1937, that certain of the San Juan Palaeocene fauna possessed "more or less opposable" thumbs' there is no palaeontological evidence of pollicial opposability (*sensu stricto*) earlier than the Pleistocene ; such evidence as exists indicates that opposability had not been acquired at any rate among the Hominoidea, by the Early Miocene. The thumb of *Proconsul africanus* had not advanced much beyond the level seen in modern *Cebus*.

It is generally agreed that opposability is an arboreal adaptation ; the corollary that all arboreal mammals have opposable thumbs is clearly not valid even when the term opposable is being employed in its most general sense ; the tree-shrews and marmosets for instance among the Primates show no evidence of opposability however widely the term is extended ; among arboreal carnivores there are of course many examples of non-opposability. Arboreal life does not necessarily involve tree-climbing and there are many arboreal forms including Primates that are of small size relative to the branches

on which they travel that may be classified to use Anthony's (1912) term as " marcheurs " or tree-runners. These forms may live at any level within the forest from the shrub layer of the forest floor to the tops of tallest emergents ; their mobility is unimpaired by the lack of prehensility, for their stability is assured by the grip of sharp claws and by the elaboration of visual and cerebellar mechanisms.

The tree-climbing phase of primate evolution may not have commenced until the middle of the Eocene, certainly there is no evidence of structural adaptation of the limbs prior to this date. The first substantial evidence that Primates had achieved this stage comes from *Notharctus* an upper Eocene lemuroid in which unequivocal arboreal adaptations are seen particularly in the foot where prehensility is apparent. The hand of *Notharctus* is much like that of a modern lemur, lacking however the widely divergent, pseudo-opposable thumb. The metacarpals are short and the phalanges long and slender ; the single terminal phalanx suggests the presence of a nail rather than a claw. All these features suggest that prehensility and probably a certain amount of pseudo-opposability of the thumb had evolved in ancestral Primates by the upper Eocene.

It would appear that among primate forms a fully prehensile hand is not acquired until a certain body size is reached. Below a critical size, clawed, convergent hands offer little or no disadvantage, but once the ratio of average branch diameter to the size of animal has reached a critical point, clawed and convergent extremities are no longer adequate to maintain stability in an arboreal environment, and some form of grasping mechanism is required. It seems possible that increase in body size comprises at least one factor in the evolution of the prehensility in the hands of Primates.

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REFERENCES

Antony, R. (1912). Contribution a l'étude morphologique générale des charactères d'adaptation à la vie arboricole chez les vertebrés. *Ann. Sci. nat.* (Zool.) (9) **15** : 101–142.

Ashton, E. H. (1960). Private communication.

Clark, W. E. Le Gros (1927). Photographs of the tree-shrew. *Proc. zool. Soc. Lond.* **1927** : 254–256.

Clark, W. E. Le Gros (1936). Problem of the claw in primates. *Proc. zool. Soc. Lond.* **1936** : 24.

Clark, W. E. Le Gros (1959). *The antecedents of man.* Edinburgh : University Press.

Day, M. H. & Napier, J. R. (1961). The two heads of flexor pollicis brevis. *J. Anat., Lond.* **95** : 123–130.

Fick, L. (1854). Quoted by Fick, R.

Fick, R. (1911). Handbuch der Anatomie und Mechanik der Gelenke III 401–405. Jena : Fischer.

Forster, A. (1916). Die Mm contrahentes und interossei manus in der Saugetierreihe und beim menschen. *Arch. Anat. Physiol.* 101–378.

Gidley, J. W. (1919). Significance of divergence of the 1st digit in the primitive mammalian foot. *J. Wash. Acad. Sci.* **9** : 273–280.

Gregory, W. K. (1951). *Evolution emerging.* New York : MacMillan.

Haines, R. W. (1944). Mechanism of rotation at the first carpo-metacarpal joint. *J. Anat., Lond.* **78** : 44–46.

Haines, R. W. (1955). Anatomy of the hand of certain insectivores. *Proc. zool. Soc. Lond.* **125** : 761.

Haines, R. W. (1958). Arboreal or terrestrial ancestry of placental mammals. *Quart. Rev. Biol.* **33** : 1–23.

Hill, W. C. O. (1955). Primates. Comparative Anatomy and Taxonomy **2** : Harplorhini Tarsioidea. Edinburgh. Univ. Press.

Hill, W. C. O. (1960). Primates. Comparative anatomy and taxonomy **4** : Cebidae, Part A. Edinburgh : Univ. Press.

Joufroy, F. K. & Lessertisseur, J. (1960). Les spécialisations anatomique de la main chez les Singes à progression suspendue. *Mammalia* **24** : 93-151.

Matthew, W. D. (1904). The arboreal ancestry of the Mammalia. *Amer. Nat.* **38** : 811–818.

Matthew, W. D. (1937). Palaeocene faunas of San Juan Basin, New Mexico. *Trans. Amer. phil. Soc.* n.s. **30.**

Midlo, C. (1934). Form of the hand and foot in Primates. *Amer. J. Phys. Anthrop.* **19** : 337–389.

Montagu. M. F. A. (1960). *An introduction to physical anthropology*, 3rd Edit. Charles C. Thomas, Springfield.

Napier, J. R. (1952). The attachments and function of the abductor pollicis brevis. *J. Anat., Lond.* **86** : 335–341.

Napier, J. R. (1955). The form and function of the carpo-metacarpal joint of the thumb. *J. Anat., Lond.* **89** : 362–369.

Napier, J. R. (1960). Studies of the hands of living Primates. *Proc. zool. Soc. Lond.* **134** : 647–657.

Napier, J. R. & Davis, P. R. (1959). The fore-limb skeleton and associated remains of *Proconsul africanus*. *Fossil mammals of Africa.* No. 16. Brit. Mus. (N.H.) Lond.

Pocock, R. I. (1918). On the external characters of the lemurs and of *Tarsius*. *Proc. zool. Soc. Lond.* **1918** : 19–53.

Pocock, R. I. (1925). Additional notes on the extreme characteristics of some platyrrhine monkeys. *Proc. zool. Soc. Lond.* **1925** : 27–47.

Polyak, S. (1957). *The vertebral visual system.* Chicago Univ. Press.

Sanderson, I. T. (1957). *The monkey kingdom.* London : Hamish Hamilton.

Woollard, H. H. (1925). The anatomy of *Tarsius spectrum*. *Proc. zool. Soc. Lond.* **1925** : 1071–1184.

GENERAL DISCUSSION

Chairman : Dr L. Harrison Matthews, F.R.S.

Dr Slijper asked if colobus monkeys were brachiating.

Dr Napier said that they were semi-brachiating. The term brachiating should perhaps be restricted to gibbons alone, but by convention it is used for chimpanzees, gorillas and the orang which are at least structural brachiators. The arm in semi-brachiators is used much more freely in moving from branch to branch than in the quadrupedal monkeys such as the African green monkeys. Dr Oxnard and Dr Ashton have worked on the shoulder girdle and have found the musculature of the langurs and the colobus monkey to be intermediate between that of the quadrupedal and the true brachiating form.

Dr Oxnard pointed out that in a different context, some of the New World monkeys, the *Ateles* and *Lagothrix* group as well as the howler monkey, show similar structural changes to those of the other semi-brachiators.

Dr O. Hill asked whether the marmoset, as an animal capable of one-handed feeding, could not be said to show opposability and mentioned that this property had been achieved much earlier in the foot than in the hand, being present even in marsupials.

Dr Napier replied that if the definition of true opposability was based on a rotation of the 1st metacarpal, most of the examples mentioned by Dr Hill, including the use of the hallux, would be defined as psuedo-opposable.

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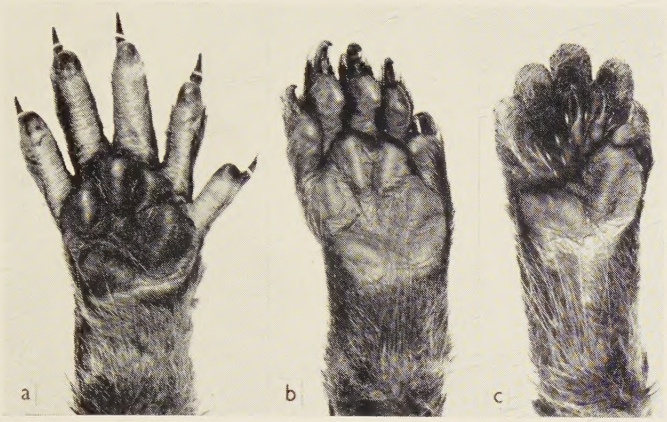

Fig. 1.—The right fore-extremity of *Trichosurus vulpecula*. (a) Divergent position (Abduction of digits); (b) semi-convergent position; (c) fully convergent position (adduction of digits).

Fig. 2.—The human hand with the digits in convergence; the thumb is fully opposed (cf. text fig. 1d).

Fig. 3.—The right fore-extremity of *Procyon lutor*.

Fig. 4.—The left fore-extremity of *Tupaia tana*.

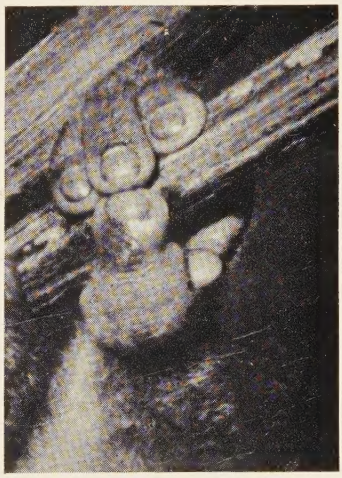

Fig. 5.—The right hand of *Perodicticus potto*.

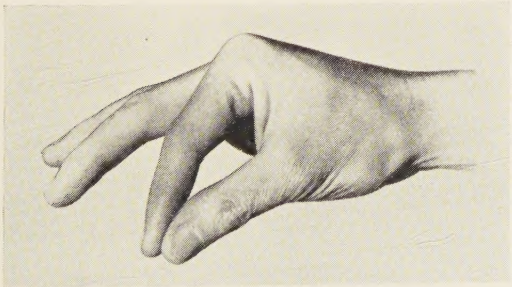

Fig. 6.—The human hand showing perfect opposability of the thumb.

Fig. 7.—Photograph shows the method of gripping sometimes employed by the orang-utan when picking up a grape from the ground.

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